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IMPRIMÉ AU DANEMARK
ANDELSBOGTRYKKERIET I ODENSE

La Morphologie Sous-Marine du Talus du Plateau Continental entre le Sud de l'Irlande et le Cap Ortegal (Espagne)

Mise au point des résultats obtenus

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Recherches Antérieures

L'étude de la topographie sous-marine du talus du plateau continental atlantique a été commencée par le Commandant BEAUGÉ sur le navire océanographique "Président-Théodore-Tissier", il y a plus de 20 ans. Mais son travail, paru en 1937, dans la *Revue des Travaux* de l'Office des Pêches Maritimes, semble inconnu à l'étranger. En effet, HILL (1956) sur la carte du NE de l'Atlantique représentant l'entrée de la Manche et le Golfe de Gascogne, ignore le travail de BEAUGÉ (1937). Cette anomalie a été récemment relevée par GUILCHER (1957) dans sa chronique océanographique de *Norois*. Il est assez surprenant de constater qu'en France même, le travail de BEAUGÉ semble également peu connu.

Les zones antérieurement sondées par BEAUGÉ comprennent:—

(a) une aire assez étendue entre les latitudes nord de 47°30′ et 49°10′ et les longitudes ouest 6°45′ et 11°10′;

(b) une aire plus restreinte intéressant la tête du canyon dit "Gouf du Cap Breton", mentionné dans tous les traités de morphologie sous-marine sans indication de l'auteur de la cartographie. Elle s'étend entre les latitudes nord 43°22′ et 43°45′ et les longitudes ouest 1°25′ et 2°05′.

Nouvelles Recherches

Les recherches ont été reprises en 1956 et 1957 à bord du "Président-Théodore-Tissier". Les premiers résultats des sondages ont été exposés dans une note préliminaire (BERTHOIS et BRENOT, 1957), mais la densité des lignes de sonde était alors beaucoup trop faible pour qu'il nous soit possible d'esquisser, même dans les grandes lignes, la topographie sous-marine du talus du plateau continental.

La campagne de 1957 a complété, par plus de 1.000 milles de sondages, les données précédemment acquises.

Les sondages ont été exécutés à l'aide d'un sondeur à ultra-sons Kelvin Hughes, pouvant atteindre la profondeur de 9.500 m par gammes de 1.500 m successives.

Nous avons procédé par passes parallèles espacées en moyenne de trois milles pour les pentes normales du talus. Des profils traversiers ont été faits fréquemment pour permettre une vérification efficace des profils parallèles. Ces profils traversiers était évidemment utilisés pour le changement de parallèle du navire. Les sondages ont eu lieu de jour et de nuit en proscrivant des changements de cap au cours de la nuit, pendant laquelle les indications du Decca sont souvent fantaisistes dans le Golfe de Gascogne.

Le point au Decca était fait toutes les demi-heures.

Les levés bathymétriques ont été reportés à l'échelle de la carte côtière du Service Hydrographique de la Marine à la même latitude. Ces échelles sont donc toutes voisines de $\frac{1}{288 \cdot 100\, \grave{e}}$

Les cartes construites sont au nombre de sept.

Les positions successives du navire ont été portées, puis vérifiées à l'aide des angles des routes suivies. Enfin les équidistances ont été contrôlées.

Nous avons été obligés très souvent de faire une sélection en n'inscrivant, sur la carte, que les altitudes les plus importantes, c'est-à-dire au moins tous les sommets, les thalwegs et les inflexions marquées du relief.

Les courbes bathymétriques n'ont été tracées qu'après exécution complète de ce travail préliminaire.

C'est à l'aide de ces cartes que nous avons dessiné la carte jointe (Fig. 1). Les principaux accidents topographiques des cartes à grande échelle y sont représentés mais nous avons dû schématiser dans de très nombreux endroits où les détails topographiques étaient trop petits pour être représentés.

Résultats

Les points suivants sont définitivement acquis:—

(1) Le talus du plateau continental est accidenté de très nombreuses vallées sous-marines entre les latitudes 49° et 44°30′N.

(2) Tous ces "canyons" ont leur origine à une profondeur sensiblement constante et toujours voisine de 200 m, avec un écart positif ou négatif qui n'exède pas 40 m.

(3) Les têtes de ces vallées sous-marines sont à environ 30 milles de la côte près du rivage des Landes mais, le plus souvent, la distance au continent est de 50 à 70 milles dans les parties médiane et nord du Golfe de Gascogne. En face de l'entrée de la Manche, la rupture de pentes est à une distance encore plus considérable.

Une seule vallée sous-marine échappe à cette règle générale, c'est le "Gouf du Cap Breton" qui s'avance jusqu'à proximité de la côte des Landes.

(4) Le long de la côte espagnole, au pied de la chaîne pyrénéenne, la topographie sous-marine n'est pas plus accusée que sur le talus de plateau continental.

(5) Au nord de la latitude de 50° jusqu'à 51°20′N, les thalwegs des vallées sous-marines ont des pentes beaucoup moins accentuées qu'au sud de la latitude 49°N.

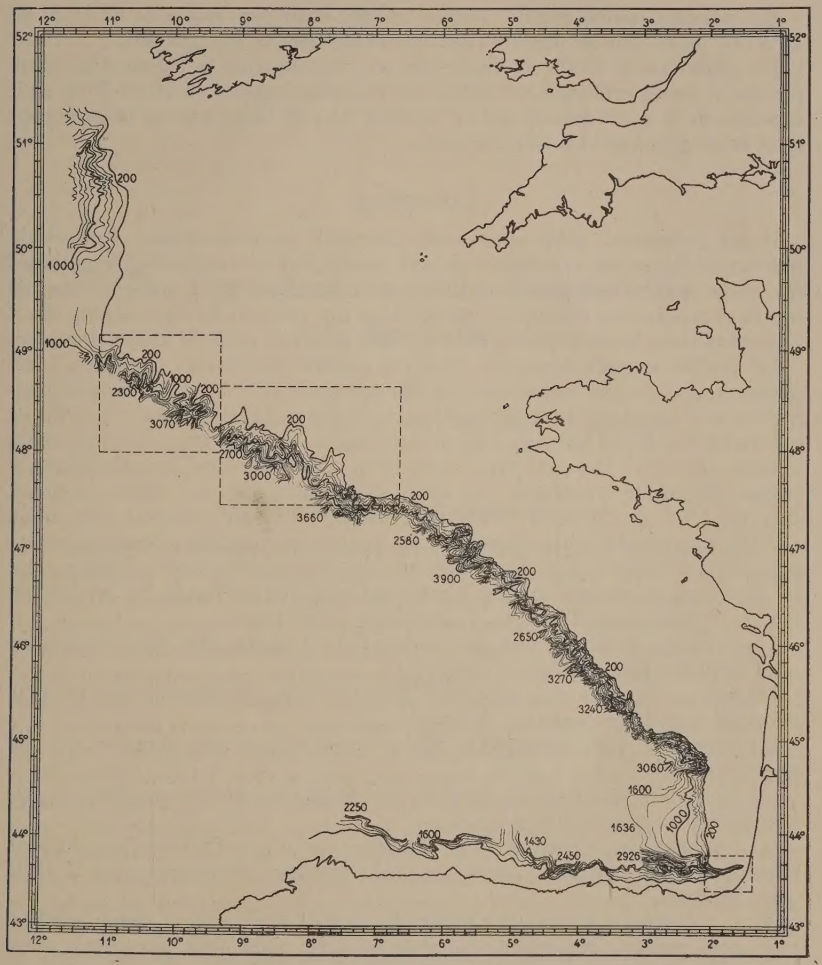

Figure 1. Topographie du talus du plateau continental entre le sud de l'Irlande et le Cap Ortegal (Espagne). Equidistance entre des courbes bathymétriques: 200 m.

(6) En de nombreux points, nos sondages ont atteint et même dépassé 3.000 m, cependant nous n'avons jamais observé un affaiblissement sensible de la vigeur du modelé sous-marin. C'est donc vraisemblablement entre 3.500 et 4.000 m que les vallées sous-marines vont enfin amortir leur topographie dans la grande fosse atlantique.

(7) Dans la région sud du Golfe, la zone limitant au nord le "Gouf du Cap Breton", forme un vaste plateau incliné vers le large, jusqu'à la profondeur de 1.600 m au moins.

Un plateau moins étendu semble exister entre les latitudes 49°10′N et 49°50′N, mais nous ne pouvons pas encore préciser sa topographie.

En définitive, le Golfe de Gascogne se présente sous la forme d'un vaste plateau à pente extrêmement faible (les isobathes tracées de 20 en 20 m sont espacées de 8 à 15 milles) qui se termine vers le large par un talus abrupt dont la morphologie est très complexe.

Conclusions

Il est prématuré d'expliquer cette disparité morphologique. Une étude sédimentologique, en voie d'achèvement, pourrait venir modifier les hypothèses que nous pourrions émettre actuellement. Cependant, il ne nous semble pas inutile d'exposer les différentes explications qui peuvent être envisagées dès à présent et entre lesquelles nous devrons faire un choix dans un avenir prochain.

Le modèle topographique du talus du plateau continental si accentué fait penser à une origine tectonique. La comparaison avec la morphologie sous-marine aux abords de la côte pyrénéenne, où nous observons une topographie semblable à celle du talus du plateau continental, ne peut que confirmer notre manière de voir. D'autre part, dans l'état actuel de nos connaissances, il paraît impossible d'expliquer un creusement subaérien des vallées jusqu'au delà de 3.000 m (Fouet et Cailleux, 1950). Mais cette origine tectonique n'exclut pas que les vallées aient été au moins partiellement occupées ensuite par des cours d'eau. Ces deux faits ne sont pas incompatibles puisque tous les géologues et sédimentologistes reconnaissent que les tracés des rivières de la côte bretonne procèdent de la tectonique armoricaine.

Les dragages profonds que nous avons faits dans les têtes de vallons nous ont fourni des galets en grand nombre.

Mais les questions qui subsistent sont les plus importantes et, pour le moment nous ne pouvons que les poser.

(a) Comment s'est constitué le plateau continental: par abrasion ou par remblaiement?

(b) Pourquoi les têtes de canyons s'arrêtent-elles presque toujours à une profondeur voisine de 200 m?

(c) Pourquoi le "Gouf du Cap Breton" qui s'avance jusqu'aux abords immédiats de la côte des Landes paraît-il constituer une exception à la règle quasi générale?

Ainsi, malgré son importance matérielle, notre travail reste encore incomplet mais nous pensons cependant que cette mise au point n'est pas inutile puisquelle permet de circonscrire le problème posé.

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The Phytoplankton of the Sargasso Sea off Bermuda*)

By

E. M. Hulburt, J. H. Ryther, and R. R. L. Guillard

Introduction and Methods

A standard oceanographic station in the north-western Sargasso Sea has been occupied at two weekly intervals since November, 1957. This station (Station S) is located fifteen miles SE of Bermuda in 1,500 fathoms of water. Routine observations have included measurements of temperature, salinity, dissolved oxygen, plant nutrients (N, P, Si), phytoplankton pigments, rates of primary production, zooplankton standing crops, light penetration, and incident solar radiation. These aspects of the programme are reported elsewhere and will be referred to here only where pertinent. In addition, each time Station S has been occupied, a series of 250 ml samples has been taken, initially from 0, 10, 25, 50, and 100 metres, later from just 0, 50, and 100 metres. These were preserved with 2% neutral formalin for subsequent examination and enumeration of the phytoplankton organisms. After the sample bottles were received in the laboratory, the cells were allowed to settle, the supernatant was decanted and an aliquot of the remaining concentrate was counted under "high-dry" magnification. For the most part these counts include only the microorganisms down to the size of 5–10 μ. The smaller organisms were largely unidentifiable by the counting technique, their systematics are unknown or uncertain and many of the delicate forms were probably destroyed or made unrecognizable by the method of preservation. This fraction of the phytoplankton will be discussed briefly at the end of the paper.

In this report we shall consider primarily the species composition, abundance, diversity, and the seasonal variation of these properties as revealed by routine counts of surface (0–10 m) samples collected each month for the period November 1957–November 1958 and of selected samples from 50 m collected within the same period.

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Results

The complete listing of species and numbers of organisms counted in this annual series is given in Tables 1 and 2. In each case the species found only at the surface or only at 50 m are indicated by asterisks. In addition, counts have been lumped into the three major algal groups present (Coccolithophoridaceae, diatoms, and dinoflagellates) to show their relative importance (Table 3). The one dominant in the region, *Coccolithus huxleyi*, is shown separately in this table. Also shown are values for chlorophyll *a*, determined from the same water that provided the phytoplankton samples, and temperatures (from MENZEL and RYTHER, in press).

Species composition and abundance

The most striking feature of the phytoplankton in the Bermuda area is the predominance of the Coccolithophoridaceae throughout the year, with a single exception, and the dominance of one species, *Coccolithus huxleyi*, for at least half the year. The latter occurred in greatest abundance in the late autumn or early winter (December, 1957 and November, 1958), but was dominant, exceeding in number all the other species combined, throughout the spring with the exception of April. It was about equally abundant at both the surface and 50 m, and appears to be associated with temperatures between 20° and 24°C (Table 3), its midsummer decline probably resulting from high temperatures. It has been shown by experiments with this species in culture that its optimum temperature for growth is about 20°C and that it will not grow above 25°C (MJAALAND, 1956).

In April, a spring flowering of moderate magnitude took place. Chlorophyll *a* values at that time were two to three times as great as were present throughout the late autumn and winter, and an order of magnitude greater than the summer values. The hydrographic features responsible for this flowering are discussed in detail elsewhere (MENZEL and RYTHER, in press), but in essence the bloom coincided with the onset of thermal stratification of the surface waters following a period of winter and early spring cooling and mixing to 300–400 m. Figure 1, from RYTHER and MENZEL (in press), shows net primary production, as measured by a simulated *in situ* ^{14}C technique, and the temperature structure of the upper 700 m, which illustrates the dependence of plant growth upon the hydrography of the surface waters.

The spring flowering was remarkable for the fact that it consisted predominantly of diatoms, this group being numerically abundant only at that one time of the year. At the surface, no single species of diatom was dominant. Of the 19 species observed, ten were present at concentrations between 1,000 and 10,000 cells/litre. At 50 m, on the other hand, there were ten times as many cells present as at the surface, and of these 86% were a small unidentified centric diatom which was not even observed in the surface sample. Unfortunately, our sampling programme did not anticipate the rapid changes which occurred at that time of year, and we have only a single observation of this diatom bloom. At best, however, it was short-lived, for by the middle of May the diatoms were outnumbered by both Coccolithophoridaceae and dinoflagellates.

The dinoflagellates were never dominant in the phytoplankton except in September when the entire population numbered only 1575 cells/litre. They

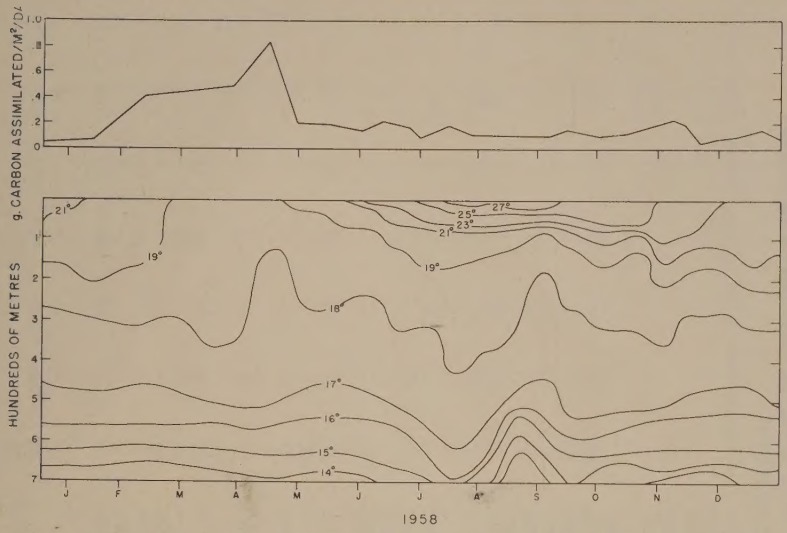

Figure 1. The annual cycle of net primary production and the temperature profile to 700 m in the Sargasso Sea off Bermuda (from RYTHER and MENZEL, in press).

were least abundant in the November–March winter period, and most numerous in the summer and early autumn. Again temperature appears to be the most likely factor controlling their presence.

In the late autumn of both 1957 and 1958 there were minor flowerings which coincided with the breakdown of the summer thermocline and the subsequent enrichment of the surface waters. In contrast to the spring diatom bloom, the autumn outburst was due entirely to an increase of one species of Coccolithophoridaceae, *C. huxleyi*.

The 50 m samples always contained a greater density of phytoplankton than the surface waters (Table 3). The difference was slight during the autumn, winter, and early spring and most pronounced when the surface waters were thermally stratified and vertical mixing presumably negligible. Of 67 species of phytoplankton observed in the surface samples, 31 or 47% were never observed at 50 m. This figure is biased, however, by the fact that more surface samples were counted. But of the 48 species observed in the 50 m samples, 14 or 29% were never seen in the more numerous surface samples. Table 4 shows, for the six times when both surface and 50 m samples were counted, the number of species found only at the surface, those found only at 50 m, and those found at both depths. While some of these differences probably resulted from inadequate counting, there being only a statistical chance of encountering rare species at both depths, there were also cases of species numerically abundant at one depth and absent from the other. Again this occurred most frequently in the summer period when vertical mixing was minimal. Under such conditions, there may be a seasonal succession of species in the upper waters, the older cells settling out and accumulating at greater depths, or mobile organisms may select depths where they are best adapted.

Table 1

Phytoplankton species and numbers in the surface waters (0–10 m) of the Sargasso Sea off Bermuda, November 1957/November 1958 (cells/litre)

	4. Nov.	3. Dec.	21. Jan.	22. Feb.	25. Mar.	15. Apr.	19. May	20. June	26. July	18. Aug.	15. Sept.	18. Oct.	14. Nov.
Bacillariophyceae:													
Bacteriastrum delicatulum	–	60	–	80	300	5800	–	–	–	–	–	–	–
**B. hyalinum*	–	–	–	–	–	1800	–	–	–	–	–	–	–
Cerataulina bergonii	–	–	–	–	–	3000	–	–	–	–	–	–	–
**Chaetoceros affinis*	–	–	–	–	–	200	–	–	–	–	–	–	–
**C. danicus*	–	–	–	–	–	–	–	–	–	15	–	–	–
**C. decipiens*	–	–	–	–	–	1000	–	–	–	–	–	–	–
**C. didymus*	–	–	–	–	–	200	–	–	–	–	–	–	–
C. laciniosus	–	–	–	–	–	1000	–	–	–	–	–	–	–
C. spp.	–	–	30	–	40	1400	–	–	–	–	–	–	–
Eucampia zoodiacus	–	–	–	–	–	1500	–	–	–	–	–	–	–
**E.* sp.	–	–	–	–	–	400	–	–	–	–	–	–	–
Hemiaulus hauckii	–	–	–	–	–	–	–	–	15	–	30	40	–
H. membranaceus	–	–	–	–	–	–	–	–	–	–	45	–	–
**Lauderia borealis* (?)	–	–	–	–	120	–	–	–	–	–	–	–	–
Leptocylindrus danicus	–	–	–	–	–	2300	–	–	–	–	–	–	–
**Nitzschia closterium* v. *recta*	–	–	–	–	–	200	–	–	–	–	–	–	–
N. delicatissima	–	–	–	–	–	1000	–	–	–	–	–	–	–
**N. seriata*	–	–	–	–	–	700	102	–	–	–	–	–	–
**Planktoniella sol*	–	–	30	–	–	–	–	–	–	–	–	–	–
**Rhabdosphaera stylifer*	–	–	–	–	–	–	–	–	–	–	–	20	–
Rhizosolenia alata	–	–	–	–	–	–	220	–	–	–	–	–	–
R. calcar avis	–	–	–	–	–	100	34	–	–	–	–	–	–
R. imbricata v. *shrubsolei*	–	30	–	–	–	–	–	–	–	–	–	–	–
R. stolterfothii	–	150	60	140	20	6500	–	–	–	–	–	–	–
**Stephanopyxis palmeriana*	–	–	–	–	40	–	–	–	–	–	–	–	–
Stigmophora rostrata	–	–	–	–	–	–	–	–	65	–	75	–	–
**Thalassionema nitzschioides*	–	210	–	–	–	–	–	–	–	–	–	–	–
**Thalassiothrix frauenfeldii*	–	–	–	–	–	300	–	–	–	–	–	–	–
**T. mediterranea*	–	–	–	–	–	600	–	–	–	–	–	–	–
Thalassiosira rotula	–	–	–	–	–	1200	–	–	–	–	–	–	–
Unidentified pennate diatoms	–	90	30	–	–	100	–	24	65	180	60	100	135
Unidentified centric diatoms	–	–	–	–	20	–	–	–	–	–	–	–	–
Chrysophyceae (Coccolithophoridaceae):													
**Braarudosphaera bigelowii*	–	–	–	–	–	–	34	–	–	–	–	–	–
Calciosolenia granii	15	–	–	–	–	–	34	–	13	–	–	–	–
**C. granii* v. *closterium*	–	–	–	–	–	–	–	–	–	–	–	–	30
Calyptrosphaera globosa (?)	–	–	–	–	80	–	612	24	13	60	30	60	15

Coccolithus huxleyi	4740	12900	2700	720	6400	200	917	1010	234	60	195	800	12600
C. leptoporus	90	60	600	20	–	–	–	192	26	15	60	160	150
**C. wallichii*	–	30	–	–	–	–	–	–	–	–	–	–	15
Deutschlandia anthos	45	–	–	–	–	–	–	–	–	–	–	–	–
Discosphaera tubifer	105	210	–	–	–	–	34	288	260	60	210	220	165
Heyneckia barkowii	–	–	–	–	–	–	–	–	13	–	–	40	–
Michaelsarsia elegans	–	30	30	–	–	–	–	–	–	–	–	–	–
M. falklandia	–	30	–	–	–	–	–	–	–	–	–	–	–
Ophiaster hydroideus	–	–	60	–	–	–	–	–	–	–	–	–	–
**Pontosphaera nigra*	–	–	–	–	–	–	–	–	–	15	–	–	–
Rhabdosphaera hispida	–	30	–	–	–	–	68	–	–	–	–	–	–
Syracosphaera heimii	–	–	90	–	20	–	374	96	–	30	–	–	120
S. pulchra	90	90	–	–	–	–	102	120	13	75	45	–	–
Umbilicosphaera mirabilis	–	30	–	–	–	–	–	–	–	–	–	–	30
Unidentified	–	–	180	–	–	–	–	48	–	45	–	–	–
Dinophyceae and Desmokontae:													
**Ceratium extensum*	–	–	30	–	–	–	–	–	–	–	–	–	–
**C. fusus*	–	–	–	–	–	–	–	–	–	–	15	–	–
**C. teres*	–	–	–	–	–	–	34	24	13	15	45	–	–
Cladopyxis setifera	–	–	–	–	–	–	–	–	–	–	–	–	30
**Dinophysis ovum*	–	–	–	–	–	300	–	–	–	–	–	–	–
**Goniodoma polyedricum*	–	–	–	–	–	–	–	–	–	–	15	–	–
Gymnodinium punctatum	–	–	30	–	–	–	–	24	–	–	–	–	–
Katodinium rotundatum	–	–	–	–	–	102	–	120	26	120	330	160	–
Oxytoxum scolopax	–	–	–	–	–	–	–	–	–	–	15	–	–
O. sphaeroideum	–	30	–	–	–	–	–	24	13	60	195	100	–
O. variabile	45	–	90	20	20	102	–	96	52	15	135	60	15
**Peridinium globulus*	15	–	–	–	–	–	–	–	–	–	–	–	–
**Podolampus palmipes*	–	–	–	–	–	–	–	–	–	15	–	–	–
**Porella perforata*	–	–	–	–	–	–	34	–	–	–	–	–	–
**Pyrocystis obtusa*	–	–	–	–	–	–	–	–	–	–	–	20	–
Unidentified	30	–	–	–	–	200	306	48	143	90	75	20	–
Chlorophyceae:													
**Carteria excavata*	–	–	30	–	–	–	–	–	–	–	–	20	–
Cryptophyceae:													
**Chilomonas marina*	–	–	–	–	–	–	–	–	–	–	–	30	–
Euglenophyceae:													
**Eutreptia* sp.	–	–	–	20	–	–	–	–	26	–	30	–	–
Myxophyceae:													
**Trichodesmium thiebaudii*	–	–	–	–	–	–	–	–	13	–	–	–	–

* Not observed at 50 m.

Table 2

Phytoplankton species and numbers at 50 m in the surface waters of the Sargasso Sea off Bermuda, November 1957/November 1958 (cells/litre)

Bacillariophyceae:	3. Dec.	21. Jan.	25. Mar.	15. Apr.	20. June	18. Aug.
Bacteriastrum delicatulum	–	–	180	–	–	–
Cerautulina bergonii	–	–	60	–	–	–
**Chaetoceros densus*	–	–	–	620	–	–
C. laciniosus	–	–	40	1860	–	–
Eucampia zoodiacus	–	–	–	620	–	–
Hemiaulus hauckii	–	–	–	–	–	13
H. membranaceus	180	–	–	–	88	–
Leptocylindrus danicus	–	–	–	620	–	–
**Nitzschia closterium*	30	–	–	620	–	–
N. delicatissima	80	–	–	7440	–	–
**Rhabdosphaera hispida*	–	–	–	–	–	104
Rhizosolenia alata	–	–	–	–	22	–
R. calcar avis	120	–	–	–	–	–
R. imbricata v. *shrubsolei*	30	–	20	–	–	–
R. stolterfothii	30	–	40	11780	–	–
**Skeletonema costatum*	–	–	–	5580	–	–
Stigmophora rostrata	–	–	–	–	22	–
Thalassiosira rotula	–	–	–	1240	–	–
Unidentified pennate diatoms	90	–	20	620	22	78
Unidentified centric diatoms	–	–	–	197160	–	–
Chrysophyceae (Coccolithophoridaceae):						
**Acanthoica acanthifera*	–	20	20	–	–	–
Calciosolenia granii	30	40	–	–	–	–
Calyptrosphaera globosa (?)	30	40	–	–	–	–
**C.* sp.	–	–	–	–	22	–
Coccolithus huxleyi	12900	2820	7540	5580	1390	–
C. leptoporus	270	540	200	620	264	64
Deutschlandia anthos	–	–	–	–	22	–
Discosphaera tubifera	210	–	–	–	396	–
Heyneckia barkowii	–	–	–	–	198	26
Michaelsarsia elegans	–	20	–	–	–	–
M. falklandia	30	80	–	–	–	–
Ophiaster hydroideus	–	240	–	–	–	–
**Pontosphaera syracusana*	–	20	–	–	–	–
Rhabdosphaera hispida	–	–	–	–	220	–
**Syracosphaera cornifera*	–	–	–	–	–	156
**S. dentata*	–	–	–	–	66	–
S. heimii	–	120	60	–	–	–
S. pulchra	120	–	–	–	220	130
Umbilicosphaera mirabilis	60	–	–	–	–	–
Unidentified	30	120	100	–	–	13
Dinophyceae and Desmokontae:						
**Ceratium pentagonium*	–	–	–	–	66	–
**C. trichoceros*	–	20	–	–	–	–
Cladopyxis setifera	–	–		–	88	13
**Exuviella baltica*	–	20	–	–	–	–
Gymnodinium punctatum	–	20	20		22	–
Katodinium rotundatum	–	–	–	–	110	234
Oxytoxum scolopax	–	–	–	–	66	–
O. sphaeroideum	–	–	–		44	130
O. variabile	–	–	–	–	242	91
**Prorocentaum dentatum*	–	–		–	22	–
**P. gracile*	–	–	–		22	–
Unidentified	–	–	20	620	176	39

* Not observed at surface.

Table 3

Relative proportions of the major groups of phytoplankton (cells/litre), chlorophyll *a* concentrations (μg/l), chlorophyll *a*/cell (mg), and water temperature (°C) at the surface and at 50 m in the Sargasso Sea off Bermuda

	4. Nov.	3. Dec.	21. Jan.	22. Feb.	25. Mar.	15. Apr.	19. May	20. June	26. July	18. Aug.	15. Sept.	18. Oct.	14. Nov.
Diatoms													
surface	–	540	150	220	540	30200	357	24	130	210	210	160	134
50 m	–	480	80	–	360	228160	–	154	–	91	–	–	–
Dinoflagellates													
surface	90	30	120	20	20	500	578	336	275	315	825	360	45
50 m	–	–	60	–	40	620	–	912	–	507	–	–	–
Coccolithophoridae (excl. *C. huxleyi*)													
surface	335	510	1020	40	100	–	1258	768	364	300	345	480	525
50 m	–	780	1270		380	620	–	1958	–	502	–	–	–
C. huxleyi													
surface	4740	12900	2700	720	6400	200	917	1010	234	60	195	800	12600
50 m	–	12900	2820		7540	5580	–	1390	–	–	–	–	–
Total cells													
surface	5165	13980	3990	1000	7060	30900	3110	2138	1003	885	1575	1800	13305
50 m	–	14160	4230		8320	234980	–	4260	–	1100	–	–	–
Ratio, no. cells													
surface/50 m		·99	·95	–	·85	·13	–	·50	–	·80	–	–	–
% dominance of most abundant single species													
surface	92	93	71	72	91	23	33	56	30	21	23	48	96
50 m	–	92	69	–	90	85	–	36	–	24	–	–	–
Chlorophyll *a*													
surface	·70	·38	·37	·34	·45	·88	·09	·07	·11	·16	·08	·24	·34
50 m	–	·47	·39	–	·48	1·00	–	·19	–	·13	–	–	–
Chlorophyll *a*/cell ($\times 10^{-8}$)													
surface	14·0	2·7	9·5	34·0	6·5	2·8	2·9	3·3	11·0	20·0	4·8	13·0	2·5
50 m	–	3·3	9·5	–	5·8	0·5	–	4·7	–	12·0	–	–	–
Temperature													
surface	24·35	22·0	20·5	18·5	18·3	18·5	21·3	24·1	28·0	28·5	27·0	25·9	23·1
50 m	–	21·6	20·4	–	18·3	18·2	–	21·5	–	24·3	–	–	–

Indeed the restriction to one or the other depth appears to be most pronounced in the dinoflagellates which are known to be migratory and depth selective in response to light (Hasle, 1950). Both Steemann Nielsen (1934) and Graham and Bronikovsky (1944) were able to differentiate between surface- and deep-dwelling species of the dinoflagellate *Ceratium*. Finally, under conditions of thermal stratification, entire populations, differing in their environmental requirements from the surface forms, may develop at these greater depths. It is impossible to decide which of these is the correct explanation without more intensive studies than we have attempted so far. The problems of vertical stratification of phytoplankton populations, settling rates in nature, depth selectivity, and vertical migration obviously need more attention. Until such time, it is difficult to conclude whether physiological differences between surface and deep-water phytoplankton, such as their responses to light (i. e. Steemann Nielsen and Hansen, 1959; Ryther and Menzel, 1959) are due to the presence of different endemic populations at these depths or to adaptation to the different environments by the same species.

Diversity

Between May and October, the total cell concentration at both the surface and at 50m was 4,000/litre or less. The ratio of concentration of the most abundant species to the total cell concentration was usually less than 0·5 or, in other words, there was less than 50% dominance. From November through March the number of cells per litre, with one exception, was greater than 4,000 and dominance by a single species was 70% or more. During the May–October, or summer period the coccolithophorid, *Discosphaera tubifer*, was dominant once and the dinoflagellate, *Katodinium rotundum* (ex *Massartia rotunda*), three times. All other summer samples and all winter samples were dominated by *Coccolithus huxleyi*. The percentage dominance by the most abundant single species is shown for each sample in Table 3.

In the counting of a phytoplankton sample, the number of species encountered normally increases at a rate roughly proportional to the logarithm of the number of individuals enumerated. If, in counting progressively larger aliquots of a given sample, the numbers of species and individuals are separately recorded, the relationship between these variables may be described by the index of diversity (α), as obtained from an expression derived by Fisher, Corbett and Williams (1943)

$$S = \alpha \log\left(\frac{N}{\alpha} + 1\right)$$

where S is the number of species and N, the number of individuals. The diversity index (α) is constant for a given population, or true sample of a population, and differs only as the number of species for a given number of individuals changes from sample to sample. Thus within a single sample, if the number of species encountered increases with the number of individuals counted, as predicted from theory, the plot of species against individuals should fall on a line of constant α. Figure 2 shows that this was the case for samples taken between May and October. If the number of species does not increase as expected, the plot of species against individuals cuts across lines of constant α. In samples taken between November and May, the observed points always cut across lines of constant α in the same way; as the number

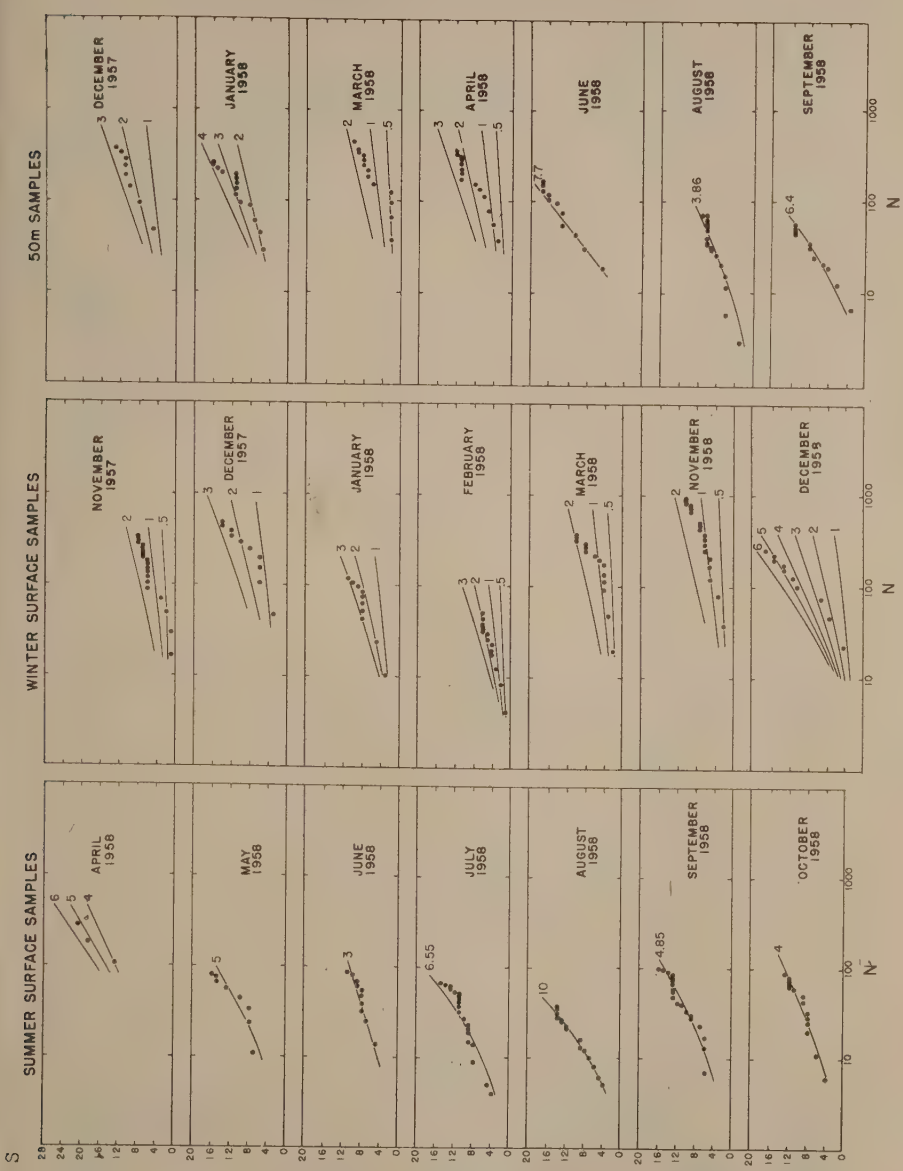

Figure 2. The index of diversity (α) of summer surface samples, winter surface samples, and 50m samples of the phytoplankton in the Sargasso Sea off Bermuda. Values of constant α are shown as numbered lines. Points show observed species-numbers relations.

of individuals counted increased, there was in every case a progressively larger number of species than expected (Figure 2).

The final value of α achieved in the winter samples ranged from three, the lower limit of the summer values, to five, well within the summer range. Thus, one is led to suspect that, if really large numbers of cells had been counted during the winter period, all the final values of α would have fallen within the summer range. The departure from theory during the winter months, then, seems to have resulted from the disproportionate growth of a single species, the same number of less abundant forms persisting from summer to winter.

Consider now the radically different situation in April. At the surface many of the species appearing in the counts were rare enough previously to have been undectectable, while many which had been prevalent at other times were now too scarce to be recorded. There were still a large number of minor species, those rarities that turn up as counting proceeds. But dominance, rather than being restricted to a single species, was shared by a dozen diatoms whose cell concentrations differed by less than an order of magnitude. At the same time, at 50 m there was a high degree of dominance (85%) by a small centric diatom not recorded at the surface or at either depth at any other time of year. Clearly, the surface and 50 m populations were quite distinct, and at both depths, different from those present throughout the rest of the year.

Discussion

From the three criteria which we have discussed, abundance, species composition, and diversity, we can describe the effects of the changing environment upon the phytoplankton community. It is probably only because these changes are gradual and relatively slight in the semi-tropical Bermuda region that we can detect and evaluate them. In any case, we see what may be interpreted as three stages in phytoplankton succession. The first, encountered during the May–October "summer" period, is characterized by a meagre population with the "normal" distribution of abundant and rare species. The physical environment may change during this period and exert selective pressure on species composition. Thus dominance passes from the Coccolithophoridaceae to the dinoflagellates as the summer progresses, probably as a result of rising temperature. But the biological environment controlling the growth of the plants (i.e. nutrients) is constant and, thus, abundance and diversity remain the same.

The second stage of succession began with the breakdown of the summer thermocline in November. The resulting enrichment of the surface waters was a slow and intermittent process; at the same time radiation was decreasing. The growth potential of the phytoplankton increased only to a limited extent, the population increasing in abundance by 2–3 fold. This increase was confined to the growth of a single species, *C. huxleyi*, which attained dominance in November and maintained it throughout the winter. Why this species was favoured over others present in nearly equal numbers in the early autumn cannot be explained. The point is, however, that the increase in the growth potential was slow enough and the environment rigorous enough to permit the selective action of some one or more chemical or physical factors upon this one species. Furthermore, throughout the ensuing winter period, growth conditions were never favourable enough to remove this selective pressure and thereby permit the general growth of the population.

Table 4

The numbers of species found only at the surface, only at 50 m, and at both depths

	Surface only	50 m only	Surface and 50 m
13. December	6	6	8
21. January	5	7	6
25. March	4	6	3
15. April	15	6	5
20. June	4	13	8
18. August.....	8	5	5

This situation changed abruptly in April with the onset of thermal stratification and the development of the third stage of succession. The phytoplankton in the euphotic zone had sudden access to nutrients and light, the growth potential increasing 10 fold over its summer level. Conditions became favourable for an entire group of plants, the diatoms. Undoubtedly, the environment favoured the growth of some species more than others, but competition and selection were unimportant for this brief period; at least a dozen diatoms could grow at rates limited mainly by their intrinsic growth potentials.

This was not the case at 50 m, however, where one species of diatom, absent from the surface, was strongly dominant. Perhaps at that depth, reduced illumination exerted sufficient selective pressure to prevent the general augmentation of the diatom population which appeared to take place at the surface.

Thus we have observed in the Bermuda waters three different types of phytoplankton communities, one consisting of sparse populations existing under marginal conditions, with the "normal" distribution of abundant and rare species; the second, living under improved but still limiting conditions, in which selective pressure favours the dominance of a single species with the minor species continuing to exist at a subsistence level; and the third, under optimal growth conditions, in which selection is largely inoperative and dominance is shared by several species. We have referred to these community types as representative of three stages of phytoplankton succession. This has the unfortunate implication that the three stages should follow each other in some regular way, and that they are interrelated. This is probably not true. It appears more likely that the communities we have described are dependent entirely upon their physical-chemical environment, and that they may follow each other in any order.

Nanoplankton

Our discussion would not be complete without some consideration of the nanoplankton or "μ"-plankton. However, the separation of this group from the phytoplankton, wholly unsatisfactory for ecological consideration to begin with, is also rather arbitrary. Thus many of the small flagellates and Coccolithophoridaceae which have been enumerated and included in our counts, as for example the dominant *Coccolithus huxleyi*, might well be included in the nanoplankton. We can only say, therefore, that we have not included in our counts a vast array of tiny microorganisms of the general size of 1–5 μ which, when looked for, are always found at a high level of numerical abundance in our samples. Of uncertain taxonomic position and mode of existence, these organisms play an unknown but almost certainly an important role in marine

ecology. In recent years many investigators have emphasized the quantitative significance of this group in the marine plankton, one of the most recent of such references by Riley (1957) relating to the north central Sargasso Sea. Our preliminary observations of nanoplankton in the Bermuda region confirm Riley's conclusions concerning the importance of this group.

While we have not attempted routine examination and enumeration of the nanoplankton (which will refer henceforth to those organisms not included in Tables 1 and 2) we have made cursory examinations of samples collected for this purpose at various times of the year. Duplicate 250 ml samples were preserved with 2% formalin and with I_2-KI in acetic acid. These were concentrated to 40 ml by sedimentation, and a 10 ml aliquot of the concentrate was placed in a Zeiss sedimentation chamber, the organisms allowed to settle again, and the concentrated organisms were then examined under 1350× magnification with a water immersion lens. One such pair of samples, collected on 2. December 1958, will be discussed briefly below.

While we could not identify most of the organisms, or frequently even place them into major taxonomic groups, we could separate the majority of the nanoplankton into the following three categories: (1) naked flagellates, small Coccolithophoridaceae, and diatoms, (2) coccoid cells about 3·5 μ in diameter, and (3) colourless filaments about 0·5 × 10–20 μ.

The first group consisted mainly of flagellates and were recognizable by their flagellae and their irregular shape. This group was better preserved by the I_2-KI except for the Coccolithophoridaceae, whose coccoliths were destroyed by the acid. The second group of thick-walled spherical cells were very uniform in size (3·5 μ) and were the most abundant form in these samples. They occurred singly or, more commonly, in clusters or sporangia-like "heads". One complete fungus-like organism observed in this sample bore a cluster of the same coccoid cells, which leads us to suspect that they are fungal spores. However, remarkably similar forms have been recently reported from the Pacific and other oceanic regions by Kriss and Mitzkevich (1958) who described them as a new class of microorganisms. The third group, the filaments, were not enumerated because they were frequently clumped. Since many of them were branched, they are suspected of being fungal mycelia. They appeared to be more abundant in the I_2-KI preservative, perhaps because the iodine-staining made them more visible.

Omitting the filaments, the counts on this one pair of samples are summarized below.

	Formalin	I_2-KI
Flagellates, small phytoplankton ..	290,000/litre	800,000/litre
"Spores"	2,900,000/litre	1,080,000/litre

Counts of this general order of magnitude have been obtained from samples collected at other times of the year in the Bermuda region. Organisms in the first category alone are thus 100 times more numerous than the phytoplankton listed in Tables 1 and 2. If the average nanoplankton were 4 μ in diameter as compared with perhaps 25 μ for the larger phytoplankton, the biomass of the two groups would be about the same. Unfortunately we do not know what fraction of the nanoplankton is autotrophic, but there is further evidence that the photosynthetic activity of this group may be far more important than that of the larger cells.

If we divide the total cell count into the chlorophyll concentration of the water, we obtain values for chlorophyll per cell ranging from 10^{-8} to 10^{-7} mg (Table 3). The lower limit is about comparable to the chlorophyll content of large diatoms, such as *Rhizosolenia alata* and *Ditylum brightwellii* (FLEMING, 1940) and one or two orders of magnitude greater than that of smaller diatoms, such as *Skeletonema costatum* and *Phaeodactylum tricornutum* (YENTSCH and RYTHER, 1959). Yet a great majority of the cells counted were *Coccolithus huxleyi*, which is smaller than any of these diatoms. If the chlorophyll values have any validity, this would indicate that our total cell counts reported in Table 3 include but a small fraction, in terms of biomass as well as numbers, of the autotrophic organisms. Thus while consideration of the larger phytoplankton alone may provide information concerning community structure and change, quantitative ecological evaluation of the autotrophic level in the sea must include all photosynthetic forms, of which the nanoplankton may be of prime importance.

Summary

1. Seasonal changes in the abundance, species composition, and diversity of the phytoplankton in the Sargasso Sea have been examined and discussed. The data are based upon a series of samples collected at monthly intervals from the surface and from 50 m at a station 15 miles SE of Bermuda.

2. Total cell counts ranged from approximately 1000 to 200,000 per litre, with lowest numbers observed in the summer (May–October), a small flowering in November, and a larger bloom in April. The population was dominated by Coccolithophoridceae during most of the year, and by a single species, *Coccolithus huxleyi*, for more than half the year. The absence of this species in summer is presumed to have resulted from high temperatures, other coccolithophorids and dinoflagellates dominating the plankton during that period. Diatoms were relatively insignificant except during the spring flowering, which lasted for no more than one month. At least 10 species of diatoms were about equally abundant in the surface waters during this bloom, while at 50 m one diatom species accounted for 85% of the total population.

3. Higher cell concentrations were invariably found at 50 m rather than at the surface, the difference being most pronounced in summer. At any one time, over half the species found either at the surface or at 50 m were not present at both depths simultaneously.

4. Three different types of community structure, as revealed by abundance, species composition, and diversity, are considered as representing three stages of phytoplankton succession.

5. The nature and significance of the nanoplankton are discussed briefly.

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Upper Lethal Temperatures for Larval Salmonids

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Introduction

Although much work has been carried out on the effect of temperature on fish, very little has been done on their early larval stages. BRETT (1956) gave a brief account on the thermal requirements of fish and the effect of temperature on their distribution. He pointed out the importance of the study of the thermal requirements during the early stages of development. The present work deals with the effect of high temperatures on larval salmonids, i. e., the early larval stages just after hatching.

Material

The fish used in these experiments were the larvae of salmon (*Salmo salar* L.), sea trout (*Salmo trutta*), and brown trout (*Salmo trutta* f. *fario*). The fish were reared at the Dove Marine Laboratory, Cullercoats, North Shields, England. Artificial fertilization was carried out either at the Laboratory or at the fish hatcheries.

Methods and Apparatus

Experiments and acclimation were carried out in 6 litre glass tanks, 8·5″ long, 7″ wide, and 15·5″ high. Thermostatically controlled glass covered electric heaters maintained temperatures within $\pm 0{\cdot}5$°C. The water was continuously aerated by compressed air and occasionally changed either by siphoning and replacing, or by introducing a continuous flow, or simply by transferring the fishes to other tanks brought to the same temperature. Salmonid larvae could live in such water for at least a fortnight without changing the water and experiments showed that at 5°C these larvae survived for three days (duration of experiment) at 3·5% oxygen saturation (BISHAI, 1959). The fish larvae used in all the experiments were reared at 5° to 6°C. Incubation of the eggs took place at an average temperature of 7·5°C.

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Effect of slow rise of temperature to upper lethal levels

Ten fish of each species (salmon, sea trout, and brown trout) were introduced into the experimental tanks. The water was heated slowly from 6°C to the desired temperature which lay between 20° to 30°C. The limit of 20°C was chosen after preliminary experiments, which showed that the larvae of the three species can live for at least one week at that temperature without any apparent ill effects.

The rise of temperature from 6°C to the desired temperature took place in 4 to 6 hours, after which the temperature was kept constant. The time at which the fish died was taken from when the desired temperature was reached. Experiments were continued either until all fish were dead or until the experiment has been running for 5 to 7 days.

Acclimation experiments

As pointed out by various authors (Huntsman, 1942; Hart, 1947; Brett, 1956) acclimation increases the resistance of fish and so produces a higher figure for the lethal temperature. Some acclimation experiments were carried out on larvae in which the yolk-sac was not completely absorbed, as when the fish reaches the fry stage other factors such as the availability of food will affect the results. Consequently acclimation had to be limited to periods not longer than 7 days. Larvae at 5°C were acclimated at 10°C and 20°C. They were held at 10°C for five days, and at 20°C for five days (two days at 10°C, two days at 15°C, and one day at 20°C). After acclimation fish were subjected to high temperatures from 22°–26°C. Tests were performed at 1°C higher temperature until two temperatures were found at one of which more than half and at the other less than half of the species tested survived. The upper lethal temperature is taken as the highest temperature that 50% of the population can withstand for 7 days (the duration of the experiment).

Experimental Results

(i) *Slow heating without previous acclimation*

The results of these experiments are shown in Table 1.

The results show that brown trout is the most resistant, salmon and sea trout less so.

(ii) *Quick transfer to higher temperatures following varying conditions of acclimation*

The results are summarized in Table 2 which again shows that brown trout is more resistant than salmon and sea trout. The median resistance time which represents 50% mortality increases with increase of acclimation temperature.

Discussion

The effect of high temperature on the survival of fish may be a direct one by being lethal. The death of fish from heat stroke was observed in nature for salmonids and other stream fishes by Huntsman (1942, 1946) and Bailey (1955). Experiments showed that salmon (*Salmo salar*), sea trout (*Salmo trutta*), and brown trout (*Salmo trutta* f. *fario*) alevins die if subjected to temperatures

Table 1

Resistance of salmon, sea trout, and brown trout alevins to high temperatures

Age: newly hatched larvae. Initial temperature 6°C (local tap water used). Fish brought to the final temperature in 6 hours period. Maximum duration of experiment: 16 days (384 hours).

Figures represent the time for 100% mortality in hours taken from when the desired temperature was reached.

Species	Temperature, °C 28	26	25	24	23	22	20
Salmo salar	2	3	15	144	192	216	No mortality
Salmo trutta	2	3	15	144	180	288	No mortality
Salmo trutta f. *fario*	5	7	15	144	200	384	No mortality

Figures represent the time for 50% mortality in hours.

Species	Temperature, °C 28	26	25	24	23	22	20
Salmo salar	1	2	10	65	120	188	No mortality
Salmo trutta	1	2	8	17	96	168	No mortality
Salmo trutta f. *fario*	1	5	12	65	144	288	No mortality

Table 2

Resistance of salmon, sea trout, and brown trout alevins to high temperatures

Age: 30 days after hatching (yolk-sac partly absorbed). Alevins transferred directly from rearing tanks to the experimental tanks (local tap water used). Duration of experiment: 7 days (168 hours).

Fish	Acclimation temp. °C	Time in hours for 50% mortality and 100% mortality (in parentheses) at different temperatures 26	25	24	23	22.5	22
Salmon	5	–	1 (1·5)	2 (14)	3 (24)	6 (30)	*
	10	1 (5)	2 (10)	12 (30)	*	*	*
	20	10 (12)	12 (14)	48 (144)	*	*	*
Sea trout	5	–	1 (1·5)	17 (62)	24 (96)	24 (125)	*
	10	1 (10)	3 (12)	48 (72)	*	*	*
	20	7 (29)	14 (35)	60 (144)	*	*	*
Brown trout	5	–	1 (3)	62 (86)	100 (126)	130 (*)	*
	10	12 (15)	24 (48)	72 (94)	*	*	*
	20	24 (144)	36 (168)	86 (168)	*	*	*

* indicates that 50% or 100% mortality was not reached before the end of the experiment.

higher than 25°C. The upper lethal limit of temperature of salmonid alevins reared at 5° to 6°C and heated slowly was barely above 23°C. Embody (1921) found that trout lived at 25°C for 10 days and at 26·7°C for three days. Rushton (1929) observed that 80% of salmon and brown trout fry died at temperatures not higher than 25°C. McGonigle (1932) found that brook trout fingerlings die at 29°C if heated slowly. Brett (1952) working on salmonids (*Oncorhynchus*) found that the upper lethal temperature of the fry acclimated at 5°C was 21·2°C–22·9°C. Moreover many investigators pointed out that young fish have a greater heat tolerance than do the adults (Huntsman, 1942; Hart, 1952, 1954; Bailey, 1955, etc.).

Acclimation of salmon, sea trout, and brown trout increases their resistance to high temperatures. The upper lethal temperature for salmon reared at 5°–6°C was 22°C but when acclimated at 10°C and 20°C it was 23°C. The results of acclimation experiments are summarized in Table 3.

Table 3

Upper lethal temperatures (°C) of salmonid alevins at different acclimation temperatures

Acclimation temperature	Upper lethal temperature (50% living for 7 days) 5°–6°C	10°C	20°C
Salmo salar	22	23	23
Salmo trutta	22	23	23
Salmo trutta f. *fario*	22·5	23	23

This table shows that by raising the acclimation temperature by 15°C (from 5°–20°C) there is a 1°C rise in the upper lethal temperature. Fry, Brett, and Clawson (1942) working with goldfish, found that for every 3°C rise in acclimation temperature the upper lethal temperature rose by about 1°C. Yearling speckled trout (*Salvelinus fontinalis*) showed a smaller change; a 7°C rise in acclimation was required to produce 1°C change in the upper lethal temperature (Fry, Hart, and Walker, 1946). This increase in the resistance to high temperatures after acclimation has been observed by many investigators (Hathaway, 1928; Sumner and Doudoroff, 1938; Brett, 1941, 1944, 1946, 1952, 1956; Fry, Brett & Clawson, 1942; Fry, Hart, and Walker, 1946; Hart, 1947, 1952).

The results of these experiments show that brown trout alevins are the most resistant to temperature changes as compared to both salmon and sea trout. Thus migratory fish seem to have less resistance to high temperatures than is indicated by lake or stream-dwelling ones. Fry, Hart, and Walker (1946) and Brett (1952, 1956) pointed out that sea migratory forms (*Oncorhynchus*) have considerably less resistance to low temperature than is indicated by lake or stream-dwelling char (*Salvelinus fontinalis*).

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Summary

1. The upper lethal temperature for salmon, sea trout, and brown trout alevins reared at 5°–6°C when heated slowly was 23°C. At 24°C, 50% lived for 5 days and at 20°C they could live without ill effects and without any mortality for at least 16 days.

2. Experiments showed that brown trout and sea trout are more resistant to high temperatures than salmon.

3. Acclimation to higher temperatures increases the upper temperature tolerance. The resistance of salmonid alevins with the yolk-sac appeared not to change with age.

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The Effect of Water Currents on the Survival and Distribution of Fish Larvae

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Introduction

Water currents are among the most important factors affecting the distribution of the pelagic larvae of fish. When hatched, the larvae have a large yolk-sac and cannot swim very well. Thus during their early stages the larvae may be passively carried by the water currents. The current not only affects the eggs and larval distribution by carrying them to different sea areas, but also indirectly affects their survival. Thus if the eggs or larvae drifted to unfavourable areas where food conditions are poor, high mortality of the brood takes place, and vice versa.

The influence of currents on the survival and distribution of eggs and larvae of sea fish was pointed out by numerous investigators (Fulton, 1897; Petersen, 1903 and 1924; Otterstrøm, 1906; Schmidt, 1909; Damas, 1909; Huntsman, 1918; Johansen, 1924, 1926, 1927, and 1929; Kramp, 1924; Runnström, 1934; Walford, 1938; Bonnet, 1939; Dannevig, 1940; Kändler, 1950; Jensen, 1952; and many others).

Graham, Carruthers, and Goodchild (1926) established a close correlation between the drift of cod eggs and larvae, and the known movements of water during 1924 in the North Sea. Russell (1937), however, showed that the dispersal of eggs and larvae which begins as a passive movement in the direction of the current soon changes into a search for their normal habit by young fish, though he did not give any evidence for his statement. Tester (1951) found that anchovy larvae were able to swim freely in later stages but were largely at the mercy of currents in the early stages of development. Bonnet (1939) concluded that cod eggs and larvae when present in the wind-agitated surface layers drift before they take to the bottom; and that the mortality due to high temperature was not a normal factor limiting the distribution and development of such eggs.

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As the surface currents are mainly caused by wind and the former affects the distribution of fish larvae, workers tried to find a correlation between year broods and early stages of development and wind force and direction. Such work has been done by THOMPSON (1930), CARRUTHERS (1938, 1951), CARRUTHERS, LAWFORD, and VELEY (1951,1953), CARRUTHERS, *et al.* (1951), and VELEY (1952). These investigators emphasized the importance of studying the current as a factor in dispersing the spawning products and indirectly affecting their survival by taking them to unfavourable areas. They found a correlation between the yearly brood and the wind prevailing during the early stages of development.

GRAHAM (1952), SIMPSON (1952), and GULLAND (1953), however, did not agree with these conclusions especially in that the critical drift given by CARRUTHERS, LAWFORD, and VELEY (1951) did not agree with the work of HENSEN and APSTEIN (1897) and GRAHAM (1926). Moreover many of the good years occurred in spite of the assumption that the fry is carried to unfavourable places. CARRUTHERS, LAWFORD, and VELEY (1953) discussed these views.

While currents affect the survival and distribution of pelagic marine fish larvae either directly or indirectly, they affect freshwater fish larvae in other ways. Thus although many freshwater larvae are pelagic and are affected by currents in their distribution, many others are demersal, i. e., they pass their early stages on the bottom of streams or rivers. An example of such larvae is that of the salmonids. My observations showed that the newly hatched larvae are incapable of active swimming in mid water because of their large yolk-sac. Although the larvae can swim for a short distance, they pass most of their time in their redds under the gravel and stones. With further development the fish become more active. This activity is shown by their ascent in the water which is however not vertical but spiral, circular, or at an angle. Once the larvae arrive near the surface they allow themselves to fall to the bottom once more.

Apparatus and Technique

No apparatus has been described in the existing literature for the study of the reaction of pelagic fish *larvae* towards a current of known velocity although adult fish and other aquatic animals have been investigated (ALLEE, 1912; SHELFORD, 1929; LYON, 1904, and 1909; CHIDESTER, 1922; GRAY, 1937; ELSON, 1939; and MCHINNON and HOAR, 1953).

The construction of a current apparatus presents many difficulties. An apparatus in which a constant uniform current is maintained for long periods requires a large supply of water. Also when experimenting with pelagic marine fish larvae, the presence of obstructions, air bubbles, etc. must be avoided as these may affect the reaction of fish towards the current. In addition, a long distance is necessary: a fish may maintain itself against a certain current for a short time but then is weakened by the current and may drift with it if it lasts for long periods. Moreover, marine fish larvae are small and transparent and difficult to observe so that an apparatus in which they can be easily seen must be used.

The present apparatus was designed to provide a reasonable water current for any required length of time. Not all conditions were fulfilled in this apparatus, however. It is characterized by the following features:—

1. It can give a constant current flow.
2. The water flow can continue for any length of time required by the investigator.
3. The direction of water flow can be reversed when required.
4. Different constant flow rates can be obtained.
5. The flow rate of the water can be determined exactly.
6. The critical current velocity at which the larvae are just able to maintain themselves against the current can be found.

Principle

A constant-level water supply feeds a straight uniform tube with a constant water flow. Larvae are introduced into the experimental tube with the least possible disturbance.

Description of apparatus

This apparatus is shown in Figure 1. The tank is supplied with sea water through the inflow B. A constant level of water is maintained in it by the overflow C situated near the top. The outflow is taken from near the bottom of A by a tube D which fits through a rubber bung. Tube D is provided with a glass T-tube which in turn is connected by wide rubber tubing and T-pieces to both ends of the experimental tube E. One branch of each T-piece is thus attached to one side of the water supply (from tube D) whilst the other is connected to an overflow tube. The two overflow tubes G and H are provided with stop-cocks, 4 and 5. These can be opened and closed as desired. Introduction of the experimental animals into the experimental tube E is done through a cup-shaped vessel F connected to one end of the experimental tube by a T-piece as shown in the figure, the connexion of the vessel F to the T-piece consisting of rubber tubing provided with a screw clip. This is only opened when introducing the larvae from F into the experimental tube E.

All glass and rubber tubing used in this apparatus were more or less of the same internal diameter, namely 1 cm. The experimental tube was about 1·5 m long and about 1·2 cm in diameter. By opening and closing the appropriate stop-cocks a constant flow of water can be obtained in one direction, and can be reversed when wanted. Thus when opening stop-cocks 1, 2, and 5 the current direction is from left to right, and from right to left when 1, 3, and 4 are opened and 2 and 5 shut.

When introducing the larvae into the experimental tube they were transferred to vessel F previously half filled up with water. Then all the stop-cocks were closed (2, 3, 4, 5) and screw-clip 6 was opened. If the larvae were carried to the bottom of the cup-shaped vessel F, they were left till they reached the experimental tube, while if the larvae were swimming at the surface slight opening of stop-cocks 4 or 5 was necessary so that the larvae were carried down into the experimental tube. Before starting an experiment, the vessel F had to be full, with no air anywhere in the apparatus. This was ensured by closing all stop-cocks except one (either 2 or 3) on that side of the experimental tube where the larvae were not present, thus water was pushed into F and filled it. Screw-clip 6 was then closed and the apparatus was ready for the experiment. The cleanliness of the water supply is very important in water current experiments. As the sea water supply in the apparatus was not very clean, filtered sea

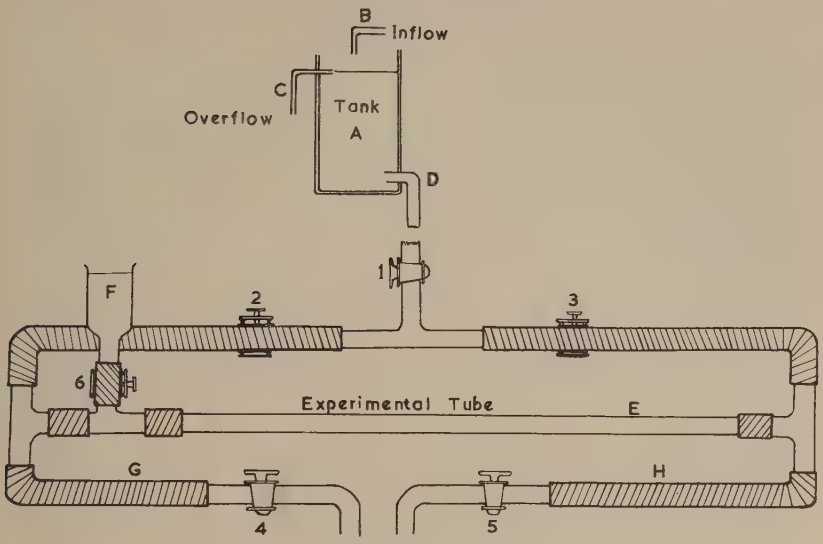

Figure 1. Apparatus used to test the reactions of fish larvae to water currents.

water was prepared for all current experiments by filtering through sand followed by glass fabric. This proved to be the most effective method although it does not free the water from very fine particles. As a strong continuous water supply was required, this was found to be the only practicable method.

Detection of water flow inside the experimental tube was done by using either a dye or milk, introduced at one end of the tube through the vessel F. The flow velocity in such a tube was found to be greatest in the middle, diminishing towards the wall.

The current apparatus described was mainly used for the study of the response of pelagic fish larvae towards different current velocities. In addition to experiments on the early stages of herring larvae, a series of experiments on lump-sucker larvae were also performed.

Calculation of the rate of water flow

The rate of the water flow can be calculated if the volume of the water passing through the experimental tube in a definite time is known. Time was measured with a stop-watch and the water collected (at either overflows G or H) in a graduated cylinder. Knowing the area of cross section of the tube, the different rates of water flow can be derived from volume measurements. In the experimental tube a flow rate of 1 mile/hour corresponds to 44·7 cm per second (area of cross section: 0·947 cm^2).

Method

Having determined the rate of flow, the fish larvae were introduced into the container F and left for some time before being introduced into the experimental

tube by the method described above. The larvae were then left in the tube for at least an hour so as to become accustomed to the new surroundings. The direction of the current flow was decided with reference to the end of the tube at which the larvae were present.

The behaviour and reactions of the larva were recorded at fixed intervals. In order to know exactly the points at which the fish reacted, the experimental tube was lined on the outside with a strip of paper divided into centimetres. When the larvae reached the other end of the tube relative to the beginning of the experiment, the flow was stopped and reversed. This was repeated at least 10 times, the larva having then travelled 50 feet. The same larva was used in 10 of such experiments (using the same flow rate), after which a new larva was introduced and the experiment repeated in the same way.

Occasionally more than one (e.g., 2–5) fish larvae were used. Individual differences within the small groups were observed but their overall reactions towards the currents were more or less uniform. A change in the rate of flow was produced by adjusting stop-cock 1, and the experiments were then repeated.

In order to determine the critical flow velocity stop-cock 1 was adjusted to produce a rate of flow at which the larvae could just maintain itself without being carried along for at least one hour.

In each experiment an attempt was made to maintain other factors such as temperature and light uniform throughout the duration of the experiment. The temperature of the water in the experimental tube was the same as that of the tanks in which the larvae were reared. It remained constant through the whole period of the experiment. In addition, the light conditions were the same as those in the rearing tanks. The experiments were peformed near the window, when dark a 100 watt bulb above the centre of the tube was used. Vibrations were avoided. The behaviour of the larvae was observed before the current flow started, and the response recorded was only that due to the current.

Material

The fish larvae used in these experiments were herring (*Clupea harengus* L.), lump-sucker (*Cyclopterus lumpus* L.), salmon (*Salmo salar* L.), sea trout (*Salmo trutta*), and brown trout (*Salmo trutta* f. *fario*). These fish larvae were reared at the Dove Marine Laboratory, Cullercoats, North Shields, England. Artificial fertilization was carried out at sea or at fish hatcheries. Experimental results in rearing of these larvae will be published later.

Rearing of the larvae took place either in glass or glazed earthenware tanks and all the experiments were carried out under the same conditions of light and temperature at which they were reared.

The average lengths of the larvae used and the temperatures at which they were reared were as follows:—

Species	Temperature °C	Length of larvae mm	Age (days)
Clupea harengus L.	13·1–14·8	6·5–8	1–9
Cyclopterus lumpus L.	10·1–13·2	6–9	1–28
Salmo salar L.	7·9–12·5	20–25	1–42*)
Salmo trutta	5–10·5	18–24	1–42*)
Salmo trutta f. *fario*	5– 9·2	16–25	1–42*)

*) Yolk-sac absorbed 28–35 days after hatching.

Experimental Results

A. Herring Larvae

Experiments were carried out on the early stages of herring larvae in which the yolk-sac was not completely absorbed (1 day to 5 days old). Older stages (up to 9 days old), however, were used, but experiments with these stages were not reliable as the yolk-sac was nearly absorbed and the larvae needed food. Most of the older larvae used in these experiments were not feeding and were weak.

In addition, herring larvae were very delicate to handle. As soon as they were transferred from the rearing tanks to the experimental tube many of them died. However, in all the experiments only the healthy larvae which behaved normally in the experimental tube were used.

1. Behaviour of larvae without current

Newly hatched herring larvae swim at random. Their swimming activity is at irregular intervals. When not swimming about they either maintain themselves near the surface or in mid water (in the rearing tanks). Swimming is by darting to and fro while moving their body (wriggling). When the larvae become older (3–7 days) they are more active and swim for longer periods, although they become weaker unless they are fed.

2. Behaviour of larvae to currents

In every case the fish orientated itself — if not at first, then in a few seconds — to face into the current whether drifting or actively swimming. Velocities investigated were 0·58 cm/sec. (0·013 mile/hour); 1·03 cm/sec. (0·023 mile/hour); 1·16 cm/sec. (0·026 mile/hour); 1·70 cm/sec. (0·038 mile/hour); 2·10 cm/sec. (0·047 mile/hour); 3·00 cm/sec. (0·067 mile/hour); 3·49 cm/sec. (0·078 mile/hour); 3·89 cm/sec. (0·087 mile/hour); 4·47 cm/sec. (0·10 mile/hour); 7·60 cm/sec. (0·17 mile/hour).

In most cases when the larvae were maintaining themselves or swimming against the current, their bodies were inclined downwards at 45° to the horizontal. In order to see if the orientation of the larvae was due to their shape, dead larvae were used in each experiment as controls. Experiments with these dead larvae showed that they drifted either head with or opposing the current and in most cases rolling, whilst the rate of drifting was in most cases higher than that of live specimens.

Movements of surrounding objects seem to have no effect on the response of herring larvae to currents. No reaction took place when passing a striped paper back and forth beneath and at the sides of the tube where the larvae were enclosed.

(i) *Response of larvae to a 0·58 cm/sec. water current*

Two newly hatched larvae were used in this experiments. The swimming larvae orientated themselves to face the current as soon as it started. The larvae remained in the middle of the tube where the current was strongest. They wriggled and maintained themselves against the current. Occasionally when the larvae ceased moving their bodies, they drifted downstream, but they neither

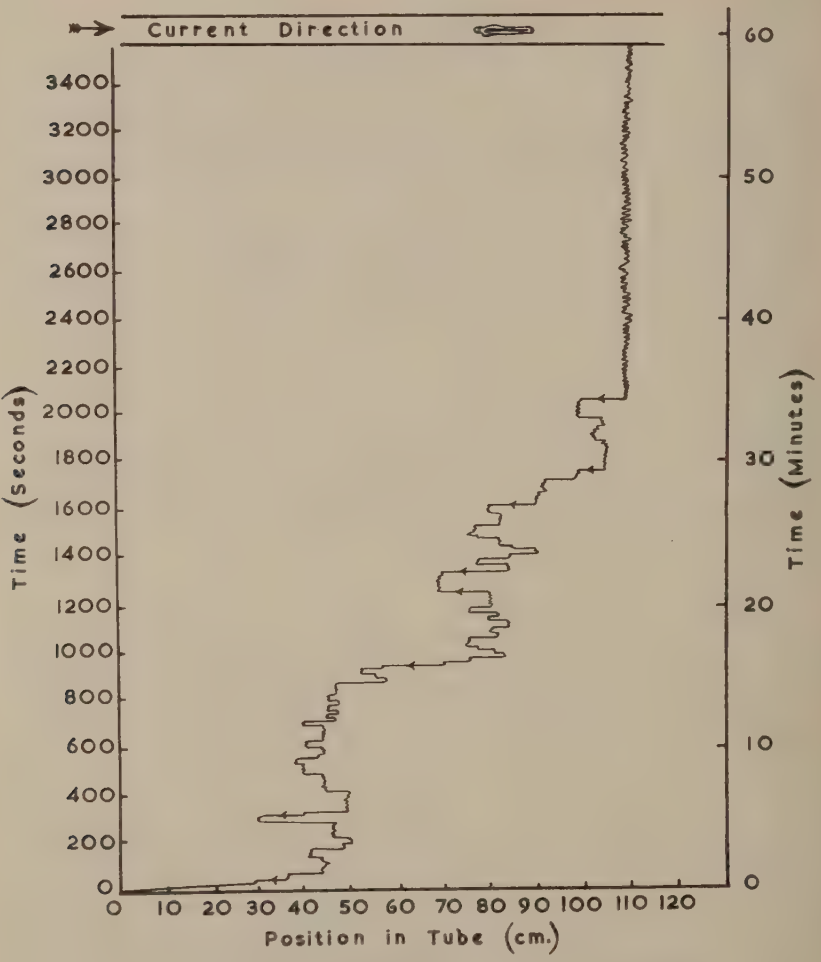

Figure 2. Response of a herring larva to a water current velocity of 2·10 cm/sec. (0·047 mile/hr).

rolled nor changed the direction of their heads. Immediately after drifting for a few centimetres they swam once more against the current and would move forward a few centimetres. In rare cases the larvae swam in the direction of the current, but soon turned to face into it and then swam against it. The larvae were not seen touching the sides of the tube.

After maintaining themselves for 14 minutes at the same spot, the larvae swam upstream and succeeded in moving a distance of 20 cm. The larvae maintained themselves against the current for at least 45 minutes without drifting from their position.

Table 1

Response of herring larvae to water currents and the relation between current velocity and drifting rate

Length of larvae: 6·5–8 mm.

Current velocity Mile/hour	Current velocity cm/sec. (A)	Average drifting rate (B) cm/sec.	$\frac{B}{A}$	Age of larvae (days)
0·013	0·58	0	0	1
0·023	1·03	0·43	0·42	1
0·026	1·16	0·62	0·53	5
0·047	2·10	0·49	0·23	6
0·067	3·00	1·48	0·49	8
0·078	3·49	1·47	0·42	1
0·087	3·89	2·6	0·66	4
0·094	4·20	3·23	0·77	8
0·10	4·47	3·15	0·70	6
0·17	7·60	4·2	0·55	1

(ii) *Response of larvae to a 2·10 cm/sec. water current*

Thirty-five experiments were carried out with different individuals at this speed and they all showed more or less the same reaction. One of the experiments is represented in Figure 2 where the abscissa represents the location of the fish (i. e., the tube divided into centimetres) while the ordinates represent the time in seconds and minutes. The diagram shows clearly *where* the larva maintained itself.

The experiment showed that the larva orientated itself throughout the experiment and attempted to swim against the current. It often succeeded in maintaining itself against the current for some time. In many cases the fish swam upstream by one dart or jump. To maintain itself at the same position the body of the fish was moving all the time. The fish remained in the middle of the tube throughout.

(iii) *Response of larvae to water current velocities higher than 2·10 cm/sec.*

More than 200 experiments were carried out with higher current velocities (i. e., 3·00, 3·49; 3·89, 4·2, 4·47, 6·25, and 7·60 cm/sec.). Table 1 shows the relationship between current velocity (cm/sec.) and drifting rate (cm/sec.). The drifting rate is defined as the distance in centimetres which the larva drifts in a second at a given current velocity. It is calculated by dividing the distance (in cm) drifted by the larva by the time in seconds. From the experiments it is possible to find out the "critical current velocity" which is the velocity at which a larva can maintain itself without being passively drifted with the current for at least one hour.

From Table 1, it can be seen that between a current velocity of 0·58 cm/sec. and 1·03 cm/sec. lies the "critical current velocity".

B. Lump-Sucker Larvae

Lump-sucker larvae have the ventral fin modified to form a sucker-like structure by which they can stick to solid objects.

About 450 experiments were carried out on early larval stages. The following current velocities were used: 7·60 cm/sec. (0·17 mile/hour); 11·18 cm/sec.

Table 2

Response of lump-sucker larvae to water current and the relation between current velocity and drifting rate

Current velocity mile/hour	Current velocity cm/sec. (A)	Average drifting rate cm/sec. (B)	Drifting rate / Current velocity B/A
0·17	7·60	6·6	0·87
0·25	11·18	13	1·16
0·50	22·35	27	1·20
0·75	33·53	38	1·13
1·00	44·70	57·7	1·29

(0·25 mile/hour); 22·35 cm/sec. (0·50 mile/hour); 33·53 cm/sec. (0·75 mile/hour); and 44·70 cm/sec. (1 mile/hour).

It was not easy to find the critical current velocity for these larvae as once the larvae were stuck to the tube by their sucker, they could withstand current velocities as high as one mile/hour. The resistance of the larvae when stuck showed that at 7·60 cm/sec. the larvae remained firm for 92 minutes and at 44·7 cm/sec. about 22 minutes.

Table 2 gives the relation between current velocity and average drifting rate.

Behaviour of the larvae to current flow

The larvae swam randomly up and down the experimental tube. Occasionally they swam the whole length of the tube at a time and then rested at the bottom. As soon as the current began the larvae either simultaneously orientated their heads to face the current or they drifted for a few seconds with their heads directed downstream, but soon turned round and opposed the current. In most cases the head remained opposing the current the whole time until the fish was carried by the current out of the experimental tube. On many occasions the larvae were seen inclined with their heads towards the bottom and their tail upwards (i.e., larvae inclined downwards at 45°). Many of the larvae attempted to stick themselves to the wall of the tube; if successful they resisted the current. When this happened the larvae usually swam upstream, then stuck fast for sometime, then again swam upstream and fastened themselves on again. In some cases when a larva was stuck fast with its head facing downstream, it orientated itself so that its head opposed the current as soon as this began to flow. In other cases, when the fish had drifted for some time with the current, it soon orientated itself to oppose it.

Experiments with recently dead larvae showed that their shape had no effect on the orientation of the larvae to current. In many cases the dead larvae drifted more slowly than the living ones due to the latter remaining mostly in the middle of the tube in the strongest current whilst the dead larvae stayed at the bottom with the least current.

Exceptionally, larvae were observed rolling with the current and just leaving themselves to its mercy without making any efforts to orientate themselves against it. The larvae did not react to any moving object outside the tube in which they are enclosed.

C. Salmon, Sea Trout, and Brown Trout Larvae

No detailed experiments were carried out on the salmonids due to technical reasons but observations in the rearing tanks showed that these larvae in the

early stages (when the yolk-sac is present up to 28 days old and rearing at 5·6°C) do not seem to respond to the current. All the time they lay on their side at the bottom of the tank darting about occasionally. Sometimes they swam for a few centimetres but they soon passed into a period of rest.

Sometimes in the pre-feeding stage when the yolk-sac is nearly absorbed, and the fish are about 35 days old, they began to react to the current and orientated themselves against it.

Using a 1·5 m length of 25 mm diameter glass tubing, a current velocity of 11·18 cm/sec. (0·25 mile/hour) caused the 35 days old alevins to orientate themselves against the current and in many cases to swim upstream. This behaviour continued till the alevins were drifted back to the other end of the tube. As soon as the current stopped they swam quickly upstream.

In the early stages (up to 21 days old) the alevins showed no reaction to any moving object outside the tube in which they were enclosed, but in later stages (pre-feeding stages) they showed a slight reaction.

Discussion

In the early stages of development fish eggs or larvae or both are carried passively by water currents prevailing during these periods, from the spawning grounds to other places. The study of the surface currents and recently the study of the wind, its velocity, direction, and duration has been carried out by many investigators. In all the studies of the effect of current on fish larvae it is supposed that these larvae are carried passively and helplessly with the current. The experimental study of the response of pelagic marine fish larvae to current, however, remains very important and may give some indications whether pelagic larvae stages are carrried entirely passively or not. Its application to natural conditions will remain uncertain until observations in nature can be carried out.

Experiments in this investigation using herring and lump-sucker larvae inside a 12 mm diameter glass tube, show that these larvae respond to currents up to 44·70 cm/sec. (higher velocities were not investigated) by orientating themselves against the current and trying to swim upstream. Herring larvae at a current velocity between 0·58 and 1·03 cm/sec. maintain themselves against the current and swim upstream, thus not drifting passively with the current. It is assumed that the critical current velocity lies between 0·58 and 1·03 cm/sec. for the early stages of herring larvae (6·5–7·5 mm long). Even at higher current velocities the rate of drifting is less than the current velocity as can be seen from Table 1, a fact explicable by the struggle of the larvae against the current and thus not being passively carried by it. It may be argued that under experimental conditions the larvae tend to choose the places with the least current velocity (near the bottom). This was not usually so, herring larvae remained in the middle of the experimental tube orientating themselves against the current and attempting to swim upstream. Only unhealthy larvae stayed at the bottom and their average drifting rate was actually higher than the average current velocity.

Whether herring larvae respond to water currents in the open sea was not studied during this investigation. Mielck (1929) showed that herring larvae were not transported by water currents from either the Dogger area or Southern Bight. Very few observations have been made in nature on the response of

pelagic fish larvae to currents. This is presumably due to difficulties involved in such observations. Cahn (1927), however, noted that *Labidesthes sicculus* larvae showed in every case an indication of orientation with a tendency on the part of the larvae to head into the waves when the surface is agitated by wind.

Demersal fish larvae, especially those living in fresh water, are affected differently from pelagic larvae. Salmon, sea trout, and brown trout alevins do not respond to current before the pre-feeding stage when they respond to currents of different velocities. Stuart (1953) made a similar observation on loch trout (*Salmo trutta*). White (1915) concluded that newly hatched brook trout are positively rheotactic. In many of her experiments, however, a number of larvae were indifferent and some even lay still on the bottom although being drifted backwards. If these larvae had been positively rheotactic they would have reacted to the current. In the present investigation it was noticed that during the pre-feeding stage salmonid larvae (salmon, sea trout, and brown trout) could perceive currents of certain velocities. In the rearing tanks most of the fish were seen near the inflow, orientating themselves against the current. Experiments on the response of salmon fry (*Oncorhynchus* sp.), were recently made by Hoar (1951, 1954) and McKinnon and Hoar (1953) who concluded that salmon fry respond positively to current and that a maximum response is shown at a particular current velocity. Specific differences were also observed.

Both marine fish larvae and salmonid fry exhibit an increased activity following an abrupt change from still water to currents or the reverse. These fish show a tendency to swim upstream as soon as the current begins. When the current ceases the fish usually continue to swim vigorously upstream. It thus seems that a change in conditions stimulates the fish to swim whilst orientation caused by current effects is responsible for the direction of their movements. A similar observation was made by Elson (1939) on young speckled trout (4–6 cm long).

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Summary

1. A review of the effect of currents on the survival and distribution of larval fish is given.

2. An experimental study on the response of fish larvae (*Clupea harengus* L., *Cyclopterus lumpus* L., *Salmo salar*, *Salmo trutta*, and *Salmo trutta f. fario*) to current, was carried out. For this purpose an apparatus was designed.

3. Experiments showed that herring and lump-sucker larvae when subjected to current in a glass tube of 12 mm diameter, are not carried passively, but

they respond positively to the current, orientate themselves against it, and try to resist it by swimming upstream.

4. For herring larvae a critical current velocity between 0·58 and 1·03 cm/sec. is found at which the larvae can maintain themselves (at least for an hour) against the current. At higher velocities the larvae are drifted with the current but the rate of drifting is less than the current velocity.

5. Salmonid larvae in the yolk-sac stage do not respond to currents. But in later stages when the yolk-sac is nearly absorbed they respond to current, orientate themselves against it and swim upstream.

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Food Habits of Larval Cod, Haddock, and Coalfish in the Gulf of Maine and Georges Bank Area

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Introduction

One of the many factors which may influence the survival of larval fish is the availability of suitable food. European investigators (LEBOUR, 1919; OGILVIE, 1938; and WIBORG, 1948) have observed that pelagic fish larvae are at times selective in their choice of food. A definite preference for a specific food form is sometimes indicated, although much of the selectivity is due to the size relationship of the larval fish and the available zooplankton.

In this paper, stomach analysis data are presented which demonstrate the relation of the food organisms and their size to larval gadoids. To avoid confusion, all the fish considered, ranging in size from 4 mm to 68 mm, are referred to as larval fish. Three species of gadoids are considered; cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; and coalfish, *Pollachius virens*.

Methods

The North Atlantic Fishery Investigations of the US Fish and Wildlife Service conducted surveys of the Gulf of Maine/Georges Bank area (Fig. 1) in the springs of 1953, 1955, 1956, and 1957 in order to measure the relative abundance of fish eggs and larvae and to relate their distribution and mortality to hydrographic conditions.

The principal plankton collecting gear used during these surveys was the Hardy Plankton Recorder. Simultaneous samples of zooplankton and fish larvae were collected from the surface with a standard one-metre net at 12 hour intervals for hatching and identification purposes. Bolting silk number 0 with an aperture of 0·57 mm was used in the metre net. This silk size retains all fish eggs and larvae endemic to the Gulf of Maine but not all of the smaller zooplankton forms. SAVILLE (1958) shows quite clearly the selectivity of various mesh sizes in plankton nets.

All larval fish and other zooplankton from the metre net tows were preserved

Figure 1. Locations of larval fish catches.

in 5% formalin. Because the emphasis of this paper is on the food of the larval fish and because the samples of these fish obtained from the tows were small, it was practical and convenient to combine the data from all the tows and cruises for each year studied. The only exception to this was in the one tow made in May 1956 in Great Harbor, Woods Hole, for comparison of the food of inshore fish with those from off shore.

The stomachs of the fish were dissected out, opened and examined grossly under low power (10×). The final sorting of organisms was done at 45×. For specimens less than 10 mm, which do not have a well defined stomach, it was necessary to examine the whole gut under 100×.

The stomach contents were identified and counted, and an estimation of the percentage volume of the different foods was made. Volumes of the zooplankton caught in the net were measured by displacement. *Centropages typicus* and *Centropages hamatus* were combined as *Centropages; Pseudocalanus minutus* and *Paracalanus parvus* as "*Pseudocalanus*-type". All stages

Table 1

Stomach contents of larval fish – "Albatross III" Cruise 61, May 1955; 75, May 1956

Cruise No. and tow No.	Location	Species	Size (mm)	Number of fish	Food
61–2	41°53′N 66°59′W	Haddock	10	1	Larval copepod remains
		Coalfish	22–24	3	*Calanus*, *Centropages*, larval copepods
61–5	43°29′N 67°29′W	Coalfish	19	1	Larval copepods
61–10	41°49′N 69°06′W	Coalfish	28–35	5	*Calanus*, "*Pseudocalanus*-type", larval euphausiids, larval copepods, unrecognizable remains
61–11	41°23′N 68°28′W	Haddock	21	1	"*Pseudocalanus*-type", *Calanus*
		Coalfish	13–24	3	"*Pseudocalanus*-type", *Calanus*, larval euphausiids
61–13	40°28′N 68°30′W	Haddock	7–16	4	Larval euphausiids, larval copepods, *Evadne*, gastropod larvae
61–16	40°26′N 70°15′W	Haddock	13	1	Larval copepods, *Calanus* (young)
61–17	40°32′N 71°24′W	Haddock	11, 25	2	"*Pseudocalanus*-type", larval copepod remains, larval euphausiids
		Coalfish	25, 26	2	Larval copepods
75–1	40°00′N 70°12′W	Haddock	4–7	5	Larval copepods
75–5	43°43′N 66°46′W	Coalfish	30, 33	2	*Calanus*, fish eggs, unrecognizable matter
75–7	43°50′N 68°10′W	Coalfish	26, 29	2	*Calanus*, *Temora*, larval copepods, larval euphausiids
		Cod	9–13	3	"*Pseudocalanus*-type", larval copepod remains
75–13	42°10′N 67°02′W	Cod	11–16	3	"*Pseudocalanus*-type", larval copepods, invertebrate eggs
		Coalfish	21–28	2	*Calanus*, "*Pseudocalanus*-type"
75–17	41°07′N 67°40′W	Cod	6–9	20	Larval copepods, invertebrate eggs, phytoplankton
		Haddock	6–9	20	Larval copepods, invertebrate eggs, phytoplankton, *Calanus* (young), pelecypod larvae
75–21	40°08′N 72°00′W	Haddock	25–46	5	"*Pseudocalanus*-type", *Temora*, *Centropages*, *Evadne*, *Oithona*, *Calanus*, larval amphipods, fish eggs

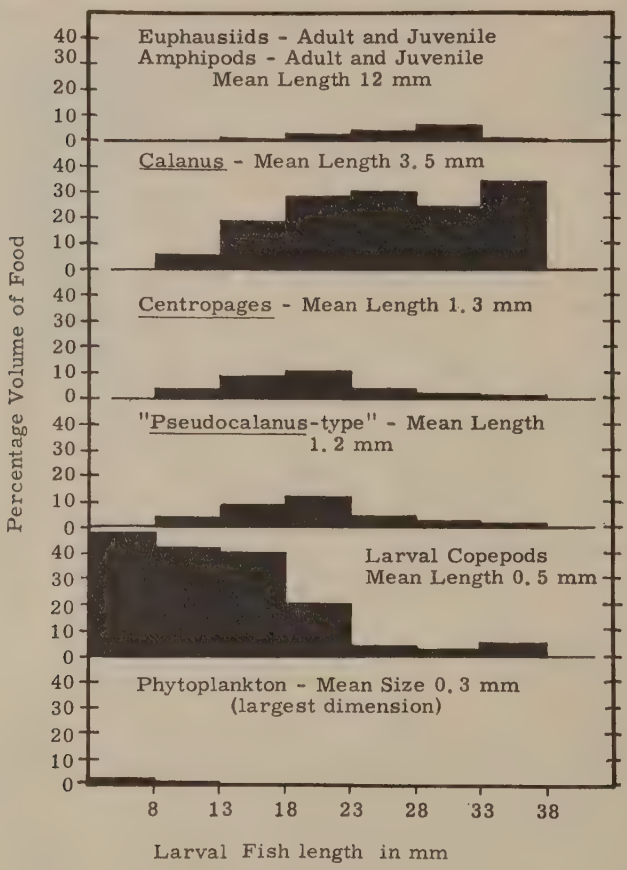

Figure 2. Percentages by volume of major types of food eaten by different size groups of larvae – 1953, 1955, 1956, 1957.

of copepods up to 0·5 mm length, euphausiids up to 8·0 mm length, and amphipods up to 6·0 mm length are listed as larvae. Because the diets of the three species are essentially similar (Table 1), especially with respect to the relation of size of larva to size of food organism, and because the diversity of times and places of collection preclude precise comparisons, data for the three gadoid species are grouped in some instances.

Results

1. Stomach contents

The most important factor in the feeding habits of the larval fish is the size of the available prey. Sizes of common food organisms are given in Table 2. As the length of the fish increases, there is generally an increase in the size

Table 2

Average length of organisms taken as food in 1953, 1955, 1956, 1957

	Average length (mm)
Copepods	
Calanus finmarchicus	3·5
Pseudocalanus minutus	1·2
Paracalanus parvus	0·8
Centropages typicus	1·3
Centropages hamatus	1·1
Metridia lucens	2·3
Temora longicornis	1·2
Eurytemora herdmani	1·2
Acartia clausi	1·0
Tortanus discaudatus	1·7
Oithona similis	0·7
Eggs and larval stages	<0·5
Harpacticoids	0·7
Euphausiids	
Meganyctiphanes norvegica	20·0
Thysanoessa inermis	11·0
Eggs and larval stages	<8·0
Amphipods	
Euthemisto compressa	15·0
Hyperia galba	12·0
Hyperia medusarum	12·0
Eggs and larval stages	6·0
Isopods	
Juveniles	3·0
Cumacea	3·5
Cladocera	
Evadne sp.	0·9
Gastropod larvae	0·2
Pelecypod larvae	0·2
Fish eggs	0·8
Fish larvae	7·0
Diatoms	0·3

of the food taken (Fig. 2). This relationship holds true for all years studied and for almost all items of food. (In the tables subsequent to Table 2, all food items are listed in order of increasing size.)

1953. During 1953, only one tow yielded appreciable numbers of fish. These 112 fish ranged in size from 9 to 28 mm. Seventy-five per cent. of the food taken by the 9 to 13 mm size group was larval copepods while *Centropages* made up the bulk of the food of the larger sizes (Table 3).

1955. The major portion of the food taken by the smallest fish (4–8 mm) was larval copepods, while the identifiable diet of the larger fish was mostly juveniles and adults of *Calanus* and "*Pseudocalanus*-type". *Centropages* contributed only 1% of the total food of all larvae (Table 4) as opposed to 54% in 1953.

1956. Stomach contents taken from 104 fish from Georges Bank and Gulf of Maine area and 119 fish caught in Great Harbor, Woods Hole, were examined. The food of the first group was a little more varied than in previous years although *Calanus* and larval copepods still comprised the bulk of the diet. As in 1955, *Centropages* made up about 1% of the food eaten. Small amounts of phytoplankton and appreciable numbers of invertebrate eggs were in the stomachs of the 4 to 8 mm size group.

Table 3

Percentage composition of stomach contents of haddock larvae from Georges Bank, 1953

	Length groups of fish (mm)						
	9–13	14–18	19–23	24–28	29–33	34–38	Total
Number of larvae	4	31	44	24	8	1	112
Phytoplankton	1	0	0	0	0	0	<1
Larval copepods	75	38	27	9	9	10	28
Temora longicornis	0	2	3	2	0	0	1
Centropages	13	42	47	64	66	90	54
Metridia lucens	0	4	1	5	9	0	3
Calanus finmarchicus	3	4	12	10	9	0	6
Amphipods	0	0	0	0	3	0	<1
Euphausiids	0	3	10	10	4	0	5
Unrecognizable	12	7	0	0	0	0	3
% empty	0	6	2	4	13	0	7
% with *Caligus*[1])	0	42	73	71	75	100	60

[1]) Ectoparasite

Table 4

Percentage composition of stomach contents of gadoid larvae, 1955

	Length groups of fish (mm)							
	4–8	9–13	14–18	19–23	24–28	29–33	34–38	Total
Number of larvae	24	11	22	35	23	8	3	126
Gastropod larvae	<1	0	0	0	0	0	0	<1
Larval copepods	93	17	4	1	5	3	17	20
Evadne sp.	<1	0	0	0	0	0	0	<1
Pseudocalanus	4	6	14	14	5	14	7	9
Fish eggs	0	0	2	1	1	0	0	1
Centropages	0	0	0	2	8	0	0	1
Calanus finmarchicus	0	26	69	77	62	50	53	48
Euphausiid larvae	2	0	0	0	2	8	0	2
Unrecognizable	0	51	11	5	17	25	23	18
% empty	4	36	22	14	0	0	0	12
% with *Caligus*[1])	0	9	9	9	26	0	33	10

[1]) Ectoparasite

The fish from Woods Hole harbour were larger than those from off shore, and their stomach contents were slightly different. *Tortanus discaudatus*, which was not present in the stomachs of the offshore fish, made up 29% of the food of the Woods Hole fish. *Centropages*, *Temora longicornis*, and larval amphipods were the other dominant food forms (Tables 5 and 6).

1957. As in 1955 and 1956, the smaller larvae were feeding almost exclusively on larval copepods. The larger fish utilized mostly juvenile and adult *Calanus* and *Centropages* (Table 7).

2. Species composition in stomachs and in metre net

In order to determine if the fish larvae are selective in their choice of food, it is necessary to compare the species composition in the stomachs to that in the environment. Such comparisons for haddock caught on Georges Bank in 1953 and coalfish caught in Woods Hole in 1956 are shown in Table 8.

Table 5

Percentage composition of stomach contents of gadoid larvae – Georges Bank, 1956

	Length groups of fish (mm)													
	4–8	9–13	14–18	19–23	24–28	29–33	34–38	39–43	44–48	49–53	54–58	59–63	64–68	Total
Number of larvae	42	24	21	3	6	4	1	0	1	1	0	0	1	104
Phytoplankton	3	0	0	0	0	0	0	–	0	0	–	–	0	<1
Pelecypod larvae	0	<1	0	0	0	0	0	–	0	0	–	–	0	<1
Invertebrate eggs	19	6	3	0	0	0	0	–	0	0	–	–	0	3
Larval copepods	69	41	37	33	0	0	0	–	0	0	–	–	0	18
Evadne sp.	0	4	0	0	0	<1	1		0	0	–	–	0	<1
Oithona similis	0	9	1	0	0	0	0	–	0	0	–	–	0	1
Fish eggs	0	0	0	33	1	5	0	–	5	30	–	–	0	7
"*Pseudocalanus*-type"	0	9	32	0	3	0	5	–	0	0	–	–	0	5
Temora longicornis	0	2	0	0	10	7	25	–	15	0	–	–	0	6
Centropages	0	0	0	0	1	0	0	–	0	0	–	–	0	<1
Calanus finmarchicus	0	8	23	33	44	45	15	–	15	30	–	–	0	22
Amphipod larvae	0	0	0	0	0	1	0	–	0	0	–	–	0	<1
Euphausiid larvae	0	0	0	0	0	5	0	–	0	0	–	–	0	<1
Amphipod adult	0	0	0	0	0	0	0	–	0	0	–	–	90	9
Unrecognizable	9	21	4	0	41	34	54	–	65	40	–	–	10	28
% empty	7	8	24	0	33	0	0	–	0	0	–	–	0	11
% with *Caligus*[1])	0	4	0	0	0	0	0	–	0	0	–	–	100	2

[1]) Ectoparasite

Table 6

Percentage composition of stomach contents of coalfish larvae – Woods Hole, 1956

	Length groups of fish (mm)					
	24–28	29–33	34–38	39–43	44–48	Total
Number of larvae	10	29	61	15	4	119
Evadne sp.	0	0	<1	<1	0	<1
Acartia clausi	<1	<1	<1	<1	0	<1
Eurytemora herdmani	3	2	3	2	0	2
Temora longicornis	11	10	10	11	9	10
Centropages	36	29	29	22	12	25
Tortanus discaudatus	28	29	28	26	40	29
Harpacticoids	<1	1	<1	0	0	<1
Calanus finmarchicus	<1	3	1	2	0	1
Isopod larvae	1	0	<1	<1	1	<1
Cumaceans	0	<1	0	0	0	<1
Post-larval fish	0	0	1	0	0	1
Amphipod larvae	1	1	1	5	24	6
Euphausiid larvae	1	2	2	3	0	1
Unrecognizable	18	23	23	27	14	24
% empty	0	0	0	0	0	0
% with *Caligus*[1])	20	10	23	0	0	16

[1]) Ectoparasite

Table 7

Percentage composition of stomach contents of gadoid larvae, 1957

	Length groups of fish (mm)							
	4–8	9–13	14–18	19–23	24–28	29–33	34–38	Total
Number of larvae	35	11	5	7	13	3	1	75
Phytoplankton	2	0	0	0	0	0	0	<1
Pelecypod larvae	2	0	0	0	0	0	0	<1
Gastropod larvae	3	0	0	0	0	0	0	<1
Invertebrate eggs	12	0	0	0	2	0	0	2
Larval copepods	80	75	100	43	7	0	0	44
Evadne sp.	0	3	0	0	0	0	0	<1
Pseudocalanus	0	0	0	36	13	0	0	7
Centropages	0	0	0	0	43	66	0	16
Calanus finmarchicus	0	0	0	21	30	10	100	23
Euphausiid larvae	0	0	0	0	0	8	0	1
Unrecognizable	1	22	0	0	5	16	0	6
% empty	17	27	0	0	0	0	0	12
% with *Caligus*[1])	0	0	0	14	15	33	0	5

[1]) Ectoparasite

Euphausiids and copepods which were the most abundant groups in the metre net samples in 1953 were generally most abundant in the stomachs of the haddock. Their order of abundance, however, differed. Although euphausiids were the dominant animals present, the fish were eating *Centropages* and larval copepods. The order of abundance of animals in the metre net samples in 1956 and in the stomachs of the coalfish was similar. The absence of adult amphipods and the greater percentage of *Centropages* and possibly *Temora* in the stomachs, however, indicates that the fish were somewhat selective in their feeding.

Although euphausiids were the most abundant food form in the 1953 sample, their size (approximately 20 mm) apparently excluded them from the diet of

Table 8

Comparison of zooplankton species in stomachs and in metre net hauls

Haddock – 1953 – Georges Bank			Coalfish – 1956 – Great Harbor, Woods Hole		
Species	% comp. metre net	% comp. stomach	Species	% comp. metre net	% comp. stomach
Euphausiids	50	5	*Tortanus discaudatus*	43	37
Centropages	15	55	*Centropages*	16	32
Metridia lucens	10	3	Adult amphipods	13	0
Calanus finmarchicus	10	6	*Temora longicornis*	7	13
Larval copepods	5	28	Larval amphipods	5	7
Amphipods	2	1	Larval euphausiids	4	1
Limacina retroversa	2	0	Adult euphausiids	3	0
Sagitta elegans	2	0	*Eurytemora herdmani*	3	3
Temora longicornis	1	1	*Calanus finmarchicus*	3	1
Candacia armata	1	0	*Pseudocalanus*	1	0
Fish eggs	1	0	*Acartia clausi*	1	1
Decapod zoea	1	0	*Evadne* sp.	1	1
			Post-larval fish	0	1
			Larval isopods	0	1
			Harpacticoids	0	1
			Cumacea	0	1

the larval haddock. The smallest haddock were feeding mainly on larval copepods (0·5 mm) while the larger haddock were feeding principally on *Centropages* (approximately 1·2 mm). There was a gradual increase in the percentage of *Centropages* and a decrease in the percentage of larval copepods in the stomachs with an increase in the size of the haddock (Table 3). In 1956 stomachs of coalfish taken from Great Harbor, Woods Hole, did not contain adult amphipods (12–15 mm) even though they were relatively abundant in the water. The coalfish also appeared to favour *Centropages* (approximately 1·2 mm) over *Tortanus discaudatus* (approximately 1·7 mm) as food (Table 8).

Discussion

The larval cod, haddock, and coalfish appear to select food of a certain size range varying with the size of fish. Lebour (1920) and Wiborg (1948) have suggested that it is the width of the food form and the size of the mouth and gullet of the fish rather than the length of the particular food that is important. We have observed in the laboratory that even if an animal can be taken into the mouth of a larval fish it is often too large to be swallowed.

The selectivity as to size of food can be summarized as follows. Prior to yolk sac absorption (at a length of approximately 4·5 mm) the larval fish feed upon copepod nauplii and very insignificant amounts of phytoplankton. From 4 to 13 mm the larvae eat mostly larval copepods, and from 13 to 23 mm principally small copepods (*Oithona* and *Centropages*) are consumed. Fish larger than 25 mm can utilize almost any size copepod and begin to eat young amphipods and euphausiids. Any one species is seldom singled out if there are others of the same size available. It is sometimes difficult to correlate the stomach contents with the available food as the fish are often captured in an environment differing from that in which they were feeding.

The seasonal variation in the plankton plays an important role in determining

the diet of larval and juvenile fish. LEBOUR (1920) found that one food item was usually predominant in the fish stomachs and in the water, and that the type of organism most abundant would often change as the season progressed. In the spring, in the Gulf of Maine and Georges Bank, when fish larvae of the species used in this study are most abundant, there are relatively more invertebrate eggs and larval copepods available. As the fish increase in size, there is a corresponding increase in the amount of larger food forms.

Not only does the type of food eaten vary with the size of the fish, but also the amount of food eaten. For example, the stomach of a 10 mm fish contained eight larval copepods whereas a 15 mm fish had eaten 18 *Centropages typicus*, and a 25 mm fish had eaten 50 *Centropages typicus*. Numbers, however, are not a true indication of the relative amount of food in the gut as one *Calanus* is equal in volume to about four *Centropages*, and a 10 mm euphausiid is equal in volume to about four *Calanus*.

A number of the larval fish examined had empty stomachs (Tables 3–7). LEBOUR (1921) has suggested that, in herring, infrequent feeding coupled with rapid digestion would account for this. SHELBOURNE (1953) demonstrated the existence of a marked diurnal pattern of feeding activity for post-larval plaice. His conclusion that plaice larvae are visual feeders holds true for other fish as most of the eighteen species taken by LEBOUR (1919) and kept alive in aquaria were observed to be feeding by sight. Larval haddock kept in an aquarium at Woods Hole have been observed to be stalking their food visually. The fact, however, that many of the haddock, cod, and coalfish taken during daylight hauls had empty stomachs indicates that feeding is sporadic and digestion rapid. One haddock larva (5 mm) observed in our laboratory ate and digested three brine shrimp (*Artemia salina*) larvae in an eight-hour period.

Many of the larval fish larger than 9 mm were parasitized by a copepod ectoparasite, *Caligus* sp. (Tables 3–7). This parasite ranged in length from 1 to 4 mm and was encountered in all areas sampled. There were as many as four parasites on some larvae, attached mostly to the first dorsal fin and the opercle. It seems unlikely that this parasitism hampers the swimming ability and hence the feeding of the larvae since the stomachs of the parasitized fish contained as much food as unparasitized fish in the same area.

Although the structure and behaviour of the prey may play an important part in determining its vulnerability, the size of the zooplankters appear to be the most important factor in their utilization as food. This is related to the size of the mouth and gullet of larval fish. The larvae are "selective" in their feeding only in that they prey upon appropriate size groups. No selection of species was observed. The data presented indicate that the fish were feeding on the most abundant species of plankton present at the time but were restricted in their choice to animals of a certain size.

Summary

1. The stomachs of 536 larval haddock, cod, and coalfish were examined. These fish were taken in a 1 metre ring-net towed horizontally through surface waters in the Gulf of Maine, on Georges Bank, and at Woods Hole during the springs of 1953, 1955, 1956, and 1957.

2. In general, larval fish were eating the most abundant species of food but were restricted to animals of a certain size.

3. Of the many kinds of food available, adults and juveniles of four species of copepods and larval copepods contributed the major portion of the diet. The composition of the food was essentially similar for all years.

4. Fish larvae ranging in size from 4 to 18 mm fed mainly on larval copepods; whereas the bulk of the food of fish larger than 18 mm was adult copepods.

5. Parasitism by *Caligus* sp. apparently did not supress feeding.

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New Implements for Fish Tagging

By

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I. The "Tagging Sluice"

In Report No. 2 on the Norwegian-Icelandic herring tagging experiments it was mentioned that double and external taggings had been introduced and some of the first results were shortly described (FRIÐRIKSSON and AASEN, 1952, p. 29). The purpose of introducing double tagging is firstly to compare the efficiency of the internal and external tags under different circumstances, and secondly to investigate the behaviour of the internal tag in the fish, the healing of the inflicted wound and so on (AASEN, 1958). Even if all earlier experience pointed towards the conclusion that properly executed taggings on herring in good condition did not harm the fish seriously, it was found advisable to treat the herring extra carefully when double taggings were to be carried out. A special apparatus has therefore been constructed. This implement (Fig. 1) has been named "The Tagging Sluice" (AASEN, 1953). It consists of four main parts:—

(a) a container for sea water and live herring (right);
(b) a sluice arrangement (middle) with sluice gates leads the herring from the container into
(c) a pivoting cradle which rests half submerged in
(d) a tagging container filled with sea water (left).

The first container or live tank is made of vulcanized, natural rubber. It is suspended in a framework of galvanized iron and rests on 7 legs with adjustable feet also made of the same material (Fig. 1). In front, towards the sluice, a small-mesh seine net is fastened to the frame and is kept to the bottom by small lead weights. This is used for guiding the fish, one at a time, head first into the sluice entrance.

When the first sluice gate (Fig. 1) is opened, the water streams into the sluice chamber and the fish follows. The sluices consist of a flat box of stainless steel and the gates are made of two plates of celluloid interlined with sponge rubber. This simple arrangement keeps the sluice chamber fairly watertight. There is a small seepage, which, however, is no particular drawback in work at sea. When the second sluice gate is opened the water flows, and carrying with it the fish, into a cradle arrangement, presently to be described (Figs. 2–5).

The cradle is made of stainless steel lined with sponge rubber modelled to fish shape. In open condition it exposes the dorsal side of the fish except the

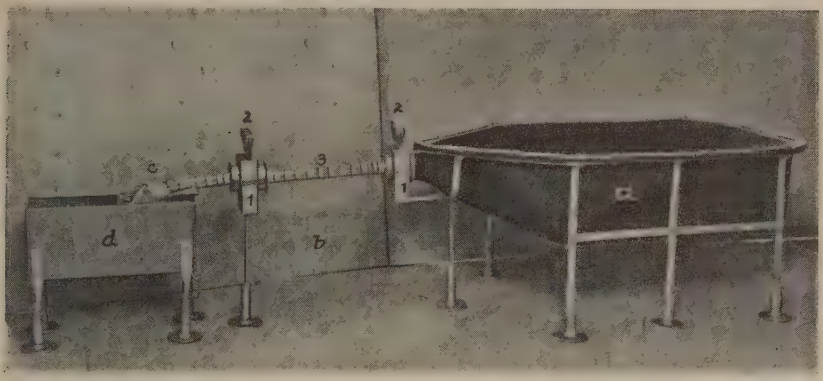

Figure 1. "The tagging sluice". (a) Container for sea water and fish. (b) Sluice arrangements: 1, sluices; 2, sluice gates; 3, chamber. Note: The second sluice is in later models mounted on the tagging container as seen in Fig. 2 and the separate supporting leg taken away. (c) Cradle. (d) Tagging container.

head which is covered. The top part of the cradle consists of two hinged flaps and a screen-lock (Fig. 2), serving dual purposes and interacting in the following manner: in forward position (Fig. 3) the screen-lock keeps the flaps apart and covers the opening next to the head part thus forming a comparatively deep channel which prevents the fish from flipping outside the cradle. In backward position (Fig. 4) the screen-lock keeps the flaps closed over the dorsal side of the fish exposing only the part between the dorsal fin and the head (where the external tag is to be fitted) and the tail (for measurement). The screen-lock is hinged on two pivots on which the cradle can be made to rotate in the vertical plane. The hinging is effected through circular holes in the lower parts of the screen-lock, slit open downwards with slits somewhat narrower than the diameters of the holes. The hinge parts of the pivots have correspondingly smaller diameters in the inner and outer parts. When mounting the screen-lock a moderate pressure at its sides will allow it to be slipped onto the pivots while the springiness of the steel keeps it locked when the pressure is released and the holes enter onto the parts with the larger diameters. Removal of the screen-lock takes place in the reverse order. The pivots on the cradle are resting on a frame sliding on the tagging container (Fig. 2). In backward position the frame brings the hind part of the cradle underneath the mouth of the sluice which also aids in keeping the hinged flaps apart (Fig. 3). In forward position the frame brings the cradle free of the sluice mouth, the flaps can be closed and the cradle made to rotate (Fig. 4). In order to accomodate fish of different lengths, there are three cradles and sluices designed to deal with the size groups 15 to 23 cm, 20 to 33 cm, and 31 to 45 cm.

The object of the rotation is to bring the fish in a position with the belly upwards for internal tagging. On the ventral side of the the cradle there is a trap door. When open, that part of the belly is exposed where the internal tag is to be inserted (immediately behind the ventral fins). For insertion of the tag is used a "tagging gun" (Fig. 5) described by FRIÐRIKSSON and AASEN (1952b, pp. 7–9).

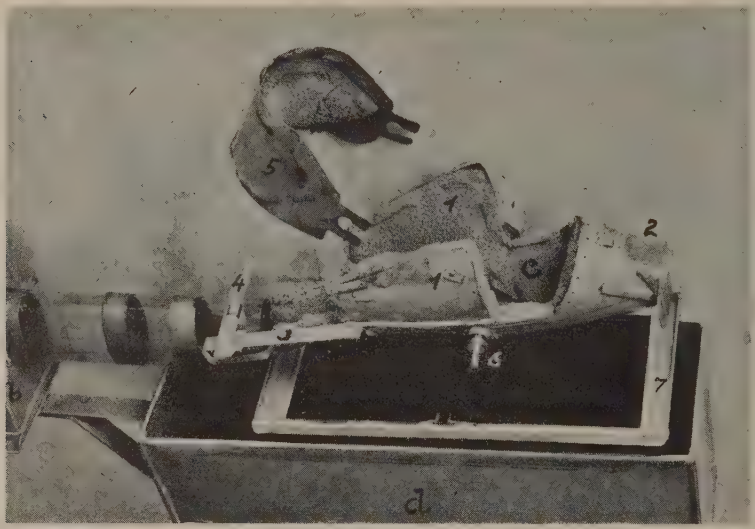

Figure 2. (b) Second sluice. (c) Cradle: 1, hinged flaps; 2, window for control during measurements, 3, ruler; 4, hinged transverse bar; 5, screen-lock; 6, pivot; 7, sliding frame. (d) Tagging container.

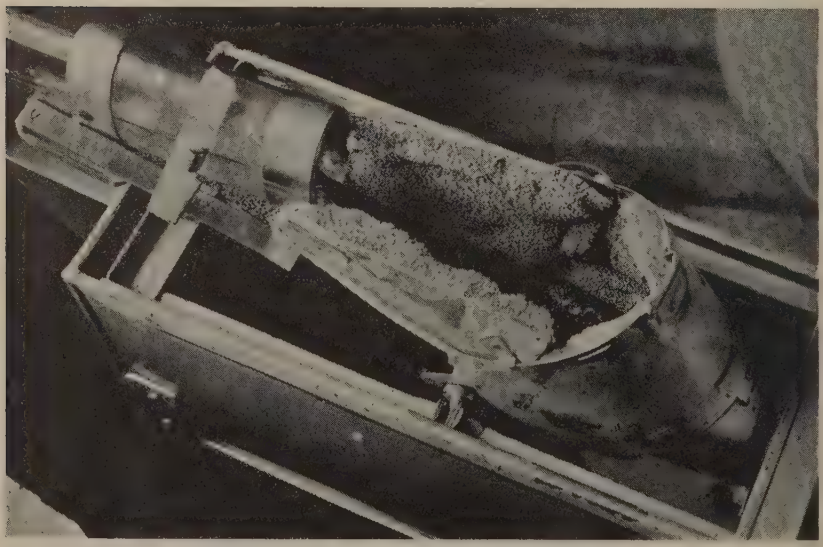

Figure 3. The screen-lock in forward position.

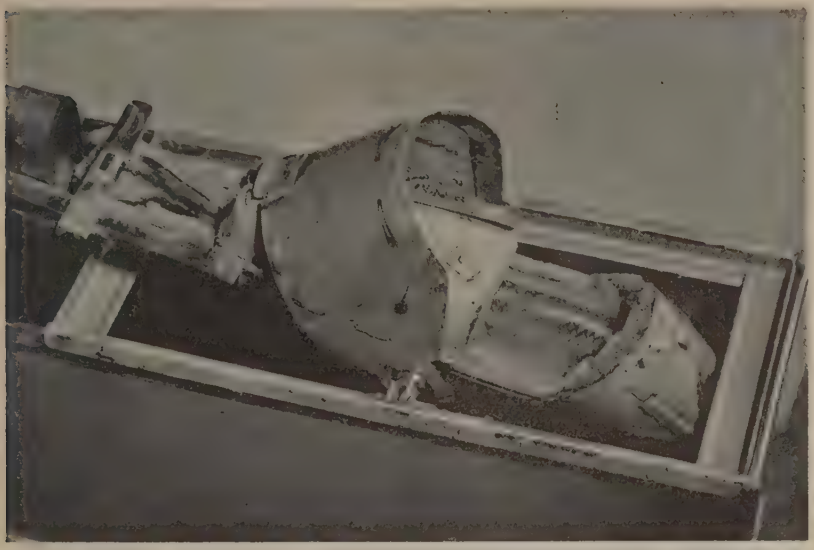

Figure 4. The screen-lock in backward position. The fish is ready for tagging and measurement.

Figure 5. Showing the fish belly up inside the cradle ready for insertion of the internal tag. The trap door, 1, is open. 2. The "tagging gun".

Figure 6. The "tagging sluice" in operation during large herring taggings in Norway in spring 1954. By courtesy of Mr. SCATTERGOOD, USA (front), in the background Mr. TIBBOE, Canada, in centre the designer of the sluice, Mr. AASEN, Norway.

Before the fish is released from the cradle length measurements may be taken and scale samples collected if so desired. A ruler is fixed to the posterior part of the cradle (Figs. 2–4). A hinged transverse bar is mounted on the ruler to ensure easy and accurate measurements. The bar is flipped aside when the fish is led into the cradle and can be moved longitudinally on the ruler, that is, the bar in measuring position moves at right angle to the ruler. To control that the snout of the fish is at the correct zero point, a window is fitted in the top head part of the cradle. The scale samples are most conveniently picked individually in the usual manner by means of forceps.

When the fish has been tagged, the lock-screen is removed, the cradle is lifted out of the frame and placed upside down into a tub with sea water placed within easy reach of the tagger (Fig. 6). The flaps are opened and the fish liberated. When a suitable quantity of fish, dependant on the size of the fish and the tub used, is reached, the tub is lowered into the sea and tipped

and the small school swims away. (The tub shown in Fig. 6 will hold about 20 fish of say 35 cm.) A similar tub is used for transferring the fish from the keep net to the live tank. The dipping of the fish from the keep net into the tub for transference to the live tank is the roughest part of the handling. It is here that the loss of scales and so forth is heaviest as the fish under such circumstances gets frantic. Otherwise, the loss of scales and other external damage to the fish is surprisingly small and quite negligible with the tagging sluice method. It has been noticed that even the slime cover on the body is not visibly damaged to any extent since the slightest pressure on the soaked sponge rubber will result in an outward flow of water.

The "tagging sluice" may be used with advantage on schooling fish species which occur with a small size range within the school. If the fish is not available in fairly great number, the process tends to become tedious, and if the size range is large it will be necessary to change over cradles and sluices during the tagging which accordingly is slowed down. Although the "tagging sluice" was designed for double tagging of fish, it naturally can be used for single tagging as well, both internally and externally.

It has been noticed during work that in the smallest size range (p. 159) the fish of 15–16 cm rather frequently get stuck in the openings for the sluice gates. There is no particular difficulties in rectifying this weakness, and indeed this has been done by GUNDERSEN (1959) in his sprat tagging experiments where a modified "tagging sluice" was employed with success. Otherwise the "tagging sluice" has been used extensively for herring tagging in Norway, and it has also been tried successfully for tagging of mackerel.

II. The "Hammock Live Container"

The live tanks in common use are almost universally rigid structures made of wood or iron or other inflexible material. These have, as well known, disadvantages on a ship under sea conditions where wave actions will tend to toss the water about in the tank, spilling some of it over the sides and otherwise make the fish inside seemingly uncomfortable, at least cause it to behave in an abnormal manner. Also (when they are not permanent installations) there are the difficulties of transporting and storing such vessels, rapidly increasing according to size. In an effort to overcome these difficulties a new type of live container has been designed and tried out in the spring of 1959 during mackerel tagging experiments in Norwegian waters.

In order to deal with the latter problem, the principle of designing a dismountable structure was employed, the impression being that more often than not, bulk is more disadvantageous than weight during transport and storage. For this size of container, the overall dimensions of the framework being $80 \times 80 \times 120$ cm, 42 mm (outer diameter) galvanized water pipes were found sufficient. The diameter of the pipes in the bottom frame is somewhat smaller, 32 mm (Fig. 7). The pipes are firmly screwed together by $\frac{1}{2}''$ screw-bolts. In order to supply good fixings for the screws, solid bolts of brass are driven into the pipes where the fixings are, and as additional support these brass strengthenings are made as shallow holes and taps in every fixture. The four legs are rubber tipped to counteract slidings on the deck of the ship. On wooden decks this has the additional advantage of not scraping during movements. The

Figure 7. The "hammock live container". (a) Legs; length: 80 cm, diameter: 42 mm, material: galvanized water pipe. (b) and (b¹) Suspending frame; lengths 120 cm and 80 cm, diameters and material as in (a). (c) and (c¹) Supporting frame; lengths, diameters, and material as in (a). (d) and (d¹) Bottom frame; lengths 102 cm and 65 cm, diameter 32 mm, material as in (a). Canvas: American, Mount Vernon No. 3. Vertical distance between suspending frame and bottom frame: 52 cm. Greatest depth (in middle): 64 cm.

framework can be erected and dismantled in five minutes. The longitudinal and transverse bars are interchangeable and so are the screw-bolts. The legs are also interchangeable, but only in pairs as will be evident from a scrutiny of Fig. 7 (and Fig. 8). This framework is absolutely rigid when properly put together. But even if the weight of the waterfilled container is sufficient to keep it in place during moderate movements of the ship, it is advisable to lash it onto the bulwark or other solid structures in case of adverse weather.

The first problem, that of water movement, has been approached by suspending a container made of canvas on the frame. In the ideal case this container should be in same position (relative to the earth) during the ship's movements, in other words, it should behave as a hammock. This has not been achieved fully in the present design, but experience at sea has shown that there is a great improvement from the conventional rigid containers, a feature which is illustrated in Figure 8, where the "hammock live container" is shown in a 15° list. The flexibility of the canvas, the movable suspension, together with the weight of the water (about 600 kg), will keep the water level in the

Figure 8. The "hammock live container" in a 15° list.

container comparatively quiet during fairly heavy wave actions both in rolling and pitching, but slightly less so if the sea is coming in on the bow or the quarter.

An ordinary pouch of canvas will enevitably take odd shapes unless it is strengthened somehow at the bottom. This question has been dealt with by introducing a bottom frame of the same material as the suspending frame (the diameter of the pipe being somewhat smaller), and screwed together in the same manner. In order to keep the extreme bottom part in shape two diagonal bars (slightly curved) are fitted onto the bottom frame as illustrated in Figure 9.

It has been preferred to make the canvas container of non-impregnated material. The reason for this is firstly that it has been noticed during tagging work that fishes (at least many of them, e.g. mackerel and herring) within certain limits, are able to change colour dorsally (FRIÐRIKSSON and AASEN, 1952, p. 16) according to the environment, making them difficult to see and catch except against a very light background in dusk or dull weather. Secondly, it may also be that the various impregnating chemicals are harmful to the fish.

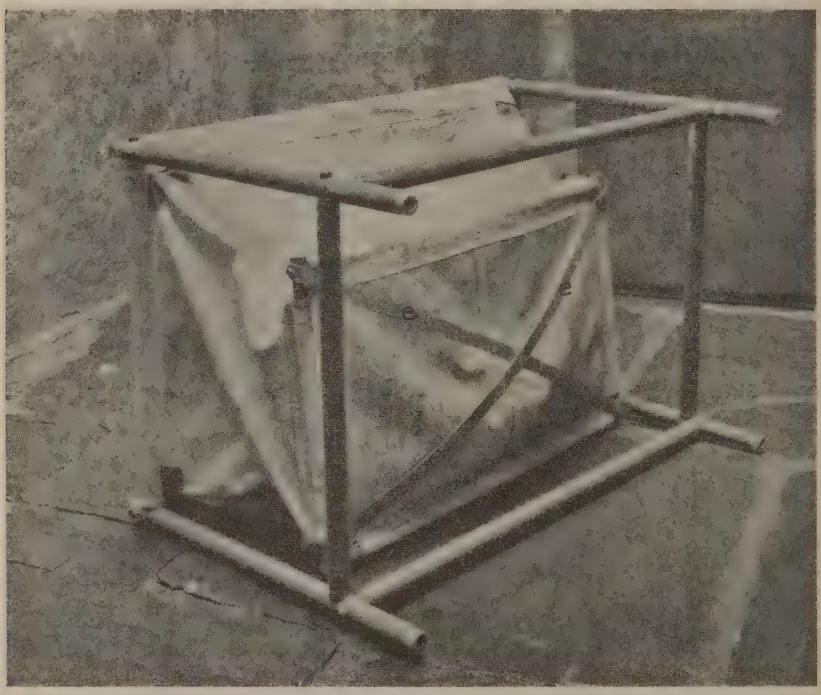

Figure 9. The "hammock live container" seen from the underside. (e) Diagonal bars; dimentions, 120×3·2×0·5 cm; material: galvanized iron.

In lack of adequate knowledge on this point, the non-impregnated material has been chosen.

For filling the "hammock live container" water from the ordinary deck cleaning pumps has been used with no visible ill-effects to the fish. For emptying the vessel a syphon of say 1″ rubber hose will do quick work.

III. Summary

Two new implements for fish tagging have been described: "The Tagging Sluice" and "The Hammock Live Container".

The first device is especially advantageous for double tagging of fish, but it may be used also for single tagging, both internally and externally. Since the fish is virtually untouched by hand during the tagging operations, the sluice is recommended for tagging of delicate fish (e.g., herring and mackerel).

The second implement's chief virtue is that it makes it possible to keep fish under sea conditions in a comparatively quiet environment. The structure can be easily dismantled for transport and storage.

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Growth of the Witch *(Glyptocephalus cynoglossus (L.))* in the Irish Sea

By

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Material and Methods

Witches were trawled off the west coast of the Isle of Man from depths between 35 and 50 fm (64 and 91m). The trawl used was a standard cotton otter trawl with all the meshes measuring $3\frac{1}{2}$ in. ($1\frac{3}{4}$ in. bar); the cod-end was covered with strong shrimp netting, 90 rows per yard. Hauls were made at irregular intervals between January 1953 and April 1956 as opportunity arose. All witches caught, a total of 1987, were taken to the laboratory.

In the laboratory the fish were measured from the tip of the snout to the end of the longest caudal fin ray and grouped in centimetre length groups, e.g. all fish between 25·0 cm and up to, but not including 26·0 cm long, were put together; for the later calculations the length of the fish in this group was taken as 25·5 cm. Sex was determined in most cases by looking at the entire fish with a strong light behind it; if there was any doubt about the form of the gonad the fish was dissected, and a squashed preparation of the gonad examined with a microscope. Sexes were separated. One saccular otolith was removed from each fish and stored in spirit in a tube labelled with the length, sex, and date of capture; otoliths from fish of one sex, in the same length group, caught on the same date, were stored together for convenience. They were subsequently cleaned by rubbing between the finger and thumb, washed in 95% spirit and placed in pure creosote in a black dish for examination by reflected light with a low-power microscope. Alternate opaque and translucent bands could be clearly seen. The appearance of each otolith was summarized by a descriptive notation recording the number of bands and the condition of the margin. Molander (1925), working in Sweden, ground witch otoliths before examining them, but this was found to be unnecessary for otoliths from witches caught near the Isle of Man provided that they were treated as described above.

Table 1

Condition of the margin of witch otoliths each month

	1953		1954		1955		1956				
	Trans-lucent	Opaque	Trans-lucent	Opaque	Trans-lucent	Opaque	Trans-lucent	Opaque	Total exam.	Total transl.	% trans-lucent
January	73	92	–	–	106	3	90	1	365	269	74
February	122	7	92	10	–	–	188	4	438	412	95
March	7	40	28	2	–	–	35	37	149	70	47
April	–	–	134	101	–	–	3	7	245	137	56
May	3	45	0	8	15	105			176	18	10
June	2	20	2	6	3	115			148	7	5
July	1	15	–	–	–	–			16	1	6
August	1	17	–	–	–	–			18	1	6
September	15	132	8	7	–	–			162	23	14
October	–	–	–	–	–	–			–	–	–
November	50	31	77	0	–	–			158	127	80
December	8	5	–	–	111	1			125	119	95

Age Determination

Otoliths of the smallest witches (6 to 9 cm long) caught in winter and early spring (November to April) had a very small nucleus lying in an opaque centre; the opaque centre was well defined and bordered by a translucent edge. Otoliths from larger fish showed a similar centre with alternate translucent and opaque bands outside it, the number of bands increasing with the size of the fish. The number of bands could be counted easily. It was evident from the records kept (Table 1) that most otoliths were translucent at the edge in the months November to April; in other words a translucent band is formed in winter. The seasonal record was not complete because sampling was irregular, but the data strongly suggest that one translucent band is formed each year in winter and one opaque band in summer. This agrees with MOLANDER's (1925) interpretation, and the annual nature of the bands will be assumed without further discussion. It follows that the age of the fish could be assessed by the number of translucent bands on the otolith.

The witch in the Irish Sea spawns in late March, April, and May. Full fish were commonest in April and spent fish in May in the samples I examined. HERDMAN (1898) reported a large number of spawning witches near the Isle of Man in April; EHRENBAUM (1905) stated that witches in the Irish Sea were ripe in April; BAL (1941), who studied fish eggs, gave the spawning period as "May to August, perhaps earlier". For the purpose of the age assessments dealt with below, April has been taken as the month in which the fish were spawned. It was therefore assumed that the small fish with otoliths showing a centre and a translucent edge but no further growth bands, were hatched in the previous April and were nearly one year old.

The witches examined were referred to their year of birth by the number of growth bands on the otolith and the date of capture; this avoided any difficulty with samples taken in the early winter and late spring when the otolith of a fish might have either an opaque or a translucent edge (because all the fish did not lay down the translucent bands at exactly the same time). In April 1954, for example, a male fish 17 cm long had an otolith which showed the centre as described above and outside the centre there was a translucent

Table 2

Monthly mean length (cm) of female witches in each age-group

(The limits shown give one standard error of the mean. The number of fish is shown in parentheses.)

Age-group	0	I	II	III	IV	V	VI	VII	VIII	IX
April	–	8·8* (7)	15·7 ± 0·2 (33)	22·8 ± 0·3 (48)	26·4 ± 0·5 (41)	30·8 ± 0·5 (20)	34·5 (3)	–	32·5 (2)	–
May	–	–	17·0 ± 0·3 (17)	22·9 ± 0·3 (67)	27·4 ± 0·4 (21)	30·5 ± 0·6 (13)	32·8 (7)	–	32·5 (1)	–
June	–	11·5 (1)	17·1 ± 0·3 (31)	23·1 ± 0·3 (46)	28·0 ± 0·5 (12)	30·5 (5)	32·5 (1)	–	–	–
July	–	13·5 (2)	18·5 (1)	25·5 (4)	30·5 (1)	–	31·0 (2)	–	–	–
August	–	–	–	26·3 (5)	27·5 (6)	–	31·8 (4)	–	–	–
September	–	12·5 (1)	–	24·8 ± 0·2 (42)	28·4 ± 0·3 (33)	29·5 (5)	34·1 (7)	34·5 (1)	–	–
October	–	–	–	–	–	–	–	–	–	–
November	–	14·8 (6)	20·7 (5)	26·6 ± 0·5 (26)	28·5 ± 0·6 (27)	31·1 ± 0·6 (10)	35·3 (4)	34·5 (1)	–	36·5 (1)
December	–	14·5 (1)	21·4 ± 0·4 (15)	26·0 ± 0·4 (28)	29·1 (5)	32·1 (5)	33·2 (3)	32·5 (1)	33·5 (1)	–
January	7·0* (2)	15·9 (7)	21·1 ± 0·3 (38)	26·3 ± 0·4 (47)	29·5 ± 0·3 (26)	31·8 ± 0·4 (34)	34·2 (3)	34·7 (5)	37·5 (1)	39·5 (1)
February	–	16·5 ± 0·5 (10)	21·9 ± 0·2 (64)	26·9 ± 0·2 (79)	29·8 ± 0·5 (22)	31·0 ± 0·4 (11)	32·2 ± 0·4 (17)	32·5 (1)	36·5 (2)	–
March	–	16·8 (3)	21·7 ± 0·3 (33)	26·6 ± 0·3 (38)	33·3 (6)	32·5 (7)	31·5 (3)	–	–	38·5 (1)

* These fish were not sexed

Table 3

Monthly mean length (cm) of male witches in each age-group

(The limits shown give one standard error of the mean. The number of fish is shown in parentheses.)

Age group	0	I	II	III	IV	V	VI	VII	VIII	IX
April	–	8·8* (7)	16·0 ± 0·3 (26)	22·4 ± 0·4 (30)	25·0 ± 0·4 (39)	25·6 ± 0·6 (12)	27·3 (5)	27·0 (2)	–	–
May	–	11·5 (1)	16·5 ± 0·2 (19)	22·3 ± 0·3 (27)	25·8 (7)	28·5 (2)	29·5 (2)	–	–	–
June	–	11·5 (1)	16·9 ± 0·2 (35)	22·3 (8)	26·6 (9)	26·5 (4)	29·5 (1)	–	–	–
July	–	13·5 (1)	–	22·3 (5)	–	–	–	–	–	–
August	–	–	–	–	–	–	–	–	–	–
September	–	–	20·8 (3)	23·6 ± 0·3 (24)	25·4 ± 0·3 (18)	27·0 ± 0·3 (10)	28·9 (7)	29·2 (6)	33·5 (1)	–
October	–	–	–	–	–	–	–	–	–	–
November	–	14·5 (7)	19·4 ± 0·6 (14)	24·1 ± 0·3 (21)	26·2 ± 0·5 (20)	28·4 (9)	28·5 (4)	29·3 (4)	–	–
December	–	15·0 (2)	19·9 ± 0·3 (18)	23·6 ± 0·5 (17)	26·7 (9)	27·1 (9)	27·5 (5)	27·2 (3)	30·5 (1)	–
January	7·0* (2)	14·1 ± 0·2 (13)	20·5 ± 0·4 (29)	25·5 ± 0·3 (80)	27·2 ± 0·3 (45)	29·8 ± 0·6 (15)	30·8 (4)	28·5 (2)	30·5 (2)	–
February	–	15·6 (8)	20·8 ± 0·3 (56)	24·5 ± 0·3 (76)	27·4 ± 0·3 (36)	27·8 ± 0·2 (19)	29·6 ± 0·4 (19)	28·8 (4)	29·5 (3)	–
March	–	15·5 ± 0·4 (12)	20·7 ± 0·5 (20)	24·9 ± 0·5 (16)	27·5 (2)	28·0 (2)	31·0 (2)	31·5 (1)	–	33·5 (1)

* These fish were not sexed

band, an opaque band, and a second translucent band forming the edge; the otolith from another fish of the same length was similar except for a narrow opaque edge of new growth outside the second translucent band; both these fish were referred to the 1952 year-class.

Growth

Mean lengths at each age-group were calculated monthly for each year-class. It became apparent that differences in growth-rate between year-classes, if any existed, could not be demonstrated from the samples obtained, and therefore length data from fish of the same age were lumped together. Mean lengths shown in Tables 2 and 3 were thus calculated from lengths of fish all at the same age but usually from more than one year-class. The number of year-classes represented is not the same at all ages because samples were not taken in every month in each year from 1953 to 1956, the period of this investigation.

Table 2 shows the monthly mean length at each age-group for the female witch, Table 3 shows similar data for males, and the points on the graphs shown in Figure 1 represent the monthly mean lengths.

Figure 1 shows that the length of female witches increases steadily and fairly rapidly from the first to the fifth year of age; thereafter the points on the graph are rather scattered but they suggest that the growth-rate declines markedly. The pattern of growth of the males is similar to that of the females, but the increase in length is not so great after the second year.

Beverton and Holt (1957) have shown that for some problems in population dynamics it is useful to describe the growth of fish in mathematical terms. The appropriate von Bertalanffy equations have been determined for growth of the witch, by using the methods described by Beverton and Holt (1957, p. 282). Annual mean lengths at each age-group were required for the calculation; it was considered that the mean of the lengths of all fish of the same age taken between October and the following September would reasonably represent the annual mean length of that age-group, since the main spawning occurred in April.

The equations calculated were, for females

$$l_t = 36{\cdot}11\,[1 - e^{-0.38\,(t-0.38)}] \qquad (1)$$

where l_t is the length in cm at age t years; and for males

$$l_t = 30{\cdot}86\,[1 - e^{-0.312\,(t-0.446)}] \qquad (2)$$

The theoretical curves are shown in Figure 1 (A and B) superimposed on the observed mean lengths, and the theoretical annual lengths are given in Table 4.

These are not the only expressions that will fit the data, though they are probably the most useful. It was found that monthly mean lengths from Tables 2 and 3 plotted against log age (in months) fell on a straight line, so the equations

$$l_m = 13{\cdot}49 \log_e m - 25{\cdot}48 \qquad (3)$$

and

$$l_m = 10{\cdot}79 \log_e m - 17{\cdot}13 \qquad (4)$$

where l_m is the length in cm at age m months, were calculated by the method of least squares from the monthly means for females and males respectively. The curves described by the equations are shown in Figure 1 (C and D).

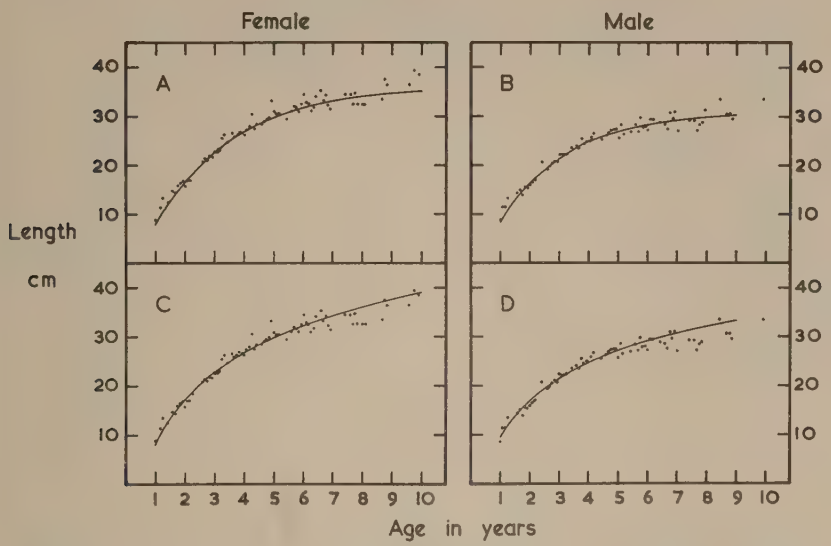

Figure 1. Theoretical growth curves superimposed on observed mean lengths. Curves A and B were obtained by fitting von Bertalanffy equations to the data for female and male witches from the Irish Sea (see text equations (1) and (2)). C and D are logarithmic curves (equations (3) and (4)).

The different pairs of theoretical curves are very similar for the middle age range where observations were numerous, but depart from each other particularly at age 8 years and above where observations were scanty. It must be remembered that the data are not derived from one year-class of fish observed over ten consecutive years but from several year-classes observed over three years; a perfect fit from any curve could hardly be expected. The curves illustrate that more than one theoretical expression may describe the growth with reasonable accuracy over a range of age for which adequate data are available.

Discussion

Fulton (1904) examined collections of witches from Scottish waters. His samples contained post-larval and very young fish taken at different times throughout the year, and he was thus able to observe the growth of young witches from the time of metamorphosis. He established that the mean length at one year of age was 9·0 cm. Length frequency analysis of samples suggested that the length at two years was about 17 cm. Fulton found difficulty in applying Petersen's method of age analysis beyond two years, but thought that the length at three years of age would probably be about 25 cm, with a range from 21 to 29 cm. The average lengths quoted by Fulton for one and two year-old witches are very similar to those I found for Manx fish (9 to 10 cm and 16 cm); this agreement supports my interpretation of otolith readings (Graham, 1929).

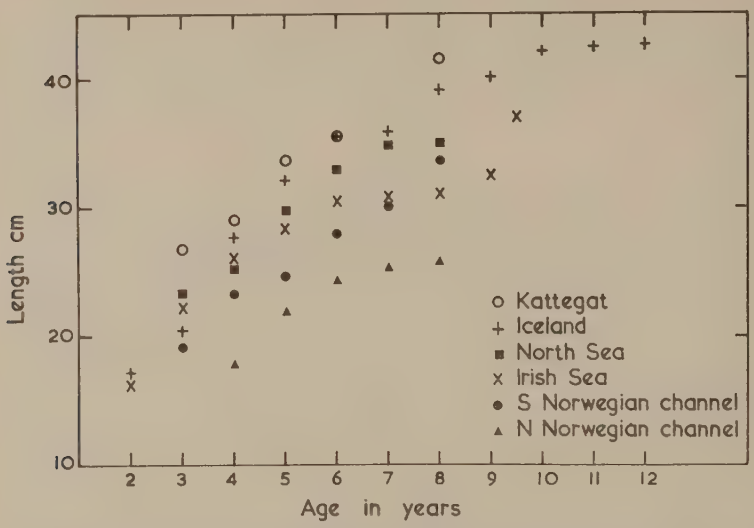

Figure 2. Mean length of witches from different seas. Age was determined by means of otoliths in all cases. Sexes are not separated. Data partly from Molander (1935) and partly from original observations.

Molander (1925, 1935), who aged fish by means of otoliths did not find witches younger than three years old in samples (presumably taken by commercial fishing gear) from the Kattegat, Skagerak, the Norwegian channel, and the northern North Sea. He showed that there was considerable difference in growth-rate of witches from these different areas. Growth of the witch in Manx waters is similar to that described by Molander for the northern North Sea and the Skagerak, but appreciably slower than growth in the Kattegat and faster than in the Norwegian channel (Figure 2). Molander found that within each area the rate of growth decreased with increasing depth. The range in depth of water fished in Manx waters was not great, and I have not investigated this phenomenon.

Molander (1935) found little difference in growth-rate between males and females, but stated that the males grew more slowly and that the difference was greatest in older fish. Fulton (1904) made no comparisons between the sexes but observed that of the smaller witches most were males, and of the larger most were females. In the present study, as shown above, it was found that there was an appreciable difference in growth-rate between males and females.

Male and female witches appear to have the same life-span, and in the Irish Sea this is about ten years. Molander (1925) recorded specimens up to fourteen years old in the Skagerak and Kattegat; these specimens were from deep water (190–250 m), mine from relatively shallow water (64–91m). Rae (1947) found witches from one to twelve years old in Scottish waters. In material sent to me from Iceland there was one 14 year-old fish, taken at a depth of 155–162 m.

Table 4

Theoretical annual length of witches

Female

Age in years	Number of fish	Mean length, cm	Length from von Bertalanffy equation (1)	Length from logarithmic equation (3)
1	13	9·73	7·71	8·04
2	109	16·41	16·41	17·39
3	387	22·64	22·77	22·86
4	332	26·85	26·99	26·73
5	129	29·85	29·86	29·74
6	91	32·03	31·84	32·21
7	31	32·92	33·19	34·28
8	11	33·68	34·11	36·08
9	4	36·0	34·74	37·67
10	3	38·2	35·12	39·10

Male

Age in years	Number of fish	Mean length, cm	Length from von Bertalanffy equation (2)	Length from logarithmic equation (4)
1	12	9·33	8·16	9·68
2	125	16·08	16·33	17·16
3	231	21·35	21·57	21·54
4	283	24·93	24·91	24·63
5	140	26·93	27·03	27·04
6	69	28·37	28·45	29·01
7	42	29·21	29·32	30·68
8	15	29·03	29·86	32·11
9	6	30·2	30·23	33·38
10	1	33·5	30·45	34·52

Table 5

Mean length at each age of witches from Iceland

Age-group	Female		Male	
	Number of fish	Mean length, cm	Number of fish	Mean length, cm
II	1	17	–	–
III	2	20·5	1	20
IV	13	27·6	6	27·5
V	11	32·0	10	31·9
VI	4	36·0	3	34·3
VII	5	36·6	6	35·0
VIII	13	39·6	4	36·5
IX	10	40·4	1	36
X	13	42·1	2	40
XI	4	42·3	–	
XII	–	–	–	
XIII	2	42·5	–	
XIV	1	48	–	

Date of sample 19. Aug. 1957. Position 64°25′5N–23°19′W and 64°23′3N–23°53′W. Depth 155–162 m and 212–225 m.

Note on Growth of the Witch in Iceland

From material kindly sent to me by Mr. Aðalsteinn Sigurðsson I have been able to estimate the rate of growth of witches in Iceland. Mean lengths at each age are shown in Table 5. There is a small difference in growth-rate between the sexes, the females growing faster. Up to four years of age, growth is similar to that in the Manx fish but thereafter Icelandic witches grow faster than the Manx fish and their growth is like that of witches from the Kattegat.

Acknowledgements

I am grateful to Mr. Aðalsteinn Sigurðsson for sending me otoliths from Icelandic witches; and to Mr. J. S. Colman and Dr. G. M. Spooner for helpful criticism of the manuscript of this paper.

Summary

1. The age of witches (*Glyptocephalus cynoglossus*) caught in the Irish Sea near the Isle of Man could readily be determined by means of otoliths.

2. Observed and theoretical growth-rates were determined. Both female and male witches grew fairly rapidly for five years and slowly thereafter. Females grew faster than males and reached a length of 36–40 cm in ten years. Males grew to about 33 cm in ten years.

3. The rate of growth observed was intermediate between the highest and the lowest growth-rates recorded for the species.

4. Examination of a sample of otoliths from Iceland indicated that witches in that area grew relatively fast.

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Mesh Selection and Apparent Growth of Haddock

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Introduction

When a sample of fish is measured and aged, it is usual to find a variation in the lengths of fish of the same age. Consider what happens when fish of the same age, but with different lengths, are incompletely retained by the meshes used in the commercial fishing gear. Large individuals are first retained at an age when the smaller individuals are still able to escape. Later, through growth, the smaller individuals become liable to capture, but, until they reach a size at which none can escape, the proportion of small fish retained at any moment is less than that of the larger fish. Therefore for a certain period in the life of the year-class, the larger fish experience a greater mortality rate than the smaller ones.

The different mortality rates of large and small fish affect the length frequency distribution by progressively reducing the relative frequencies of the larger individuals. By the time the fish are large enough to be completely retained, the mean length of the year-class is smaller than it would have been if no selection bias had been operating.

The magnitude of the bias depends on a number of factors operating during the period of incomplete retention. These are: (1) the differences in growth-rate between individuals of the same age, (2) the variance of the individual lengths at each age, (3) the average rate of growth, and (4) the intensity of fishing.

At any moment in the life of a year-class, some fish are bigger than others. This can be measured by determining the variance of the lengths at each age; this is found to increase with age as demonstrated in Figure 1 for haddock in two areas of the North Sea: the Buchan Deeps off the Scottish east coast, which is a fast growth area, and the northern North Sea basin, which is a slow growth area.

The increase in the variance of the lengths with age is considerable and needs to be explained. One possible explanation is that there is a continuous variation in the rate of growth of each fish so that any individual may be a fast grower at one moment and a slow grower at another. Movements could contribute to this if the fish are sometimes on good feeding grounds and sometimes on poor.

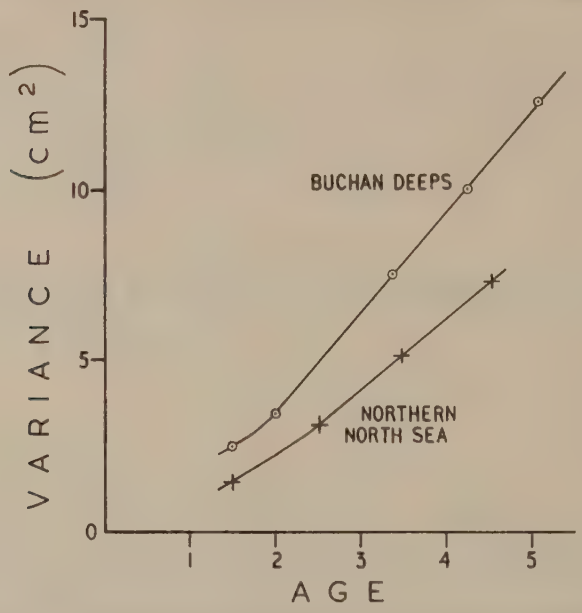

Figure 1. Relationship between the age and the variance of the lengths of North Sea haddock.

Another possibility is that some individuals are naturally faster growers than others and that, other things being equal, they remain so for their whole lives. This is a commonly observed phenomenon in many animals and plants, and evidence that it happens in haddock can be obtained by making back calculations from the scales, of the lengths at younger ages. Many samples of North Sea haddock have been analysed in this way. These show that large haddock at a given age, tend to have larger L_1 values than smaller haddock of the same age. In other words, the haddock which are relatively large at age one, tend to be relatively large at subsequent ages. This fact, coupled with the fact that the variance of the lengths increases with age, suggests that different fish grow at different rates throughout their lives and that their individual growth curves diverge from one another.

This conclusion, if correct, has one important implication. Suppose a fish, two centimetres larger than the mean is eliminated when the year-class is two years old. The absence of this fish when the year-class is older, is equivalent to the absence of a fish which would have been more than two centimetres larger than the mean. In other words, the selection bias will continue to increase even after the year-class has wholly grown through the period of incomplete retention.

The probable divergence of the individual growth curves is therefore an important factor, but, as it happens, not one that is easy to allow for in a theoretical treatment. What has been done, as a first approximation, is to make the following assumptions: –

(a) that during the period of incomplete retention the growth curves of individual fish are parallel with a slope that is constant and equal to the mean rate of growth during the period;

(b) that subsequent to the period of incomplete retention, the individual growth curves diverge in a way associated with the rate of increase in the standard deviation of the lengths.

From the first assumption it is possible to determine the magnitude of the selection bias at an age at which the smallest fish in the year-class is just large enough to be wholly retained. From the second assumption it is possible to determine the subsequent increase in selection bias with age.

Immediate Effect

Hypothetical growth curves of individual fish during the period of incomplete retention of a year-class are shown diagrammatically in Figure 2. The period of incomplete retention extends from the moment the largest fish reaches a length L_a cm until the smallest reaches a length L_b cm. The lengths L_a and L_b cm represent therefore the 0% and the 100% retention lengths of the selection curve of the cod-end concerned.

An expression is derived in the Appendix for the magnitude of the selection bias at an age t_x which is defined as the age at which the smallest individuals

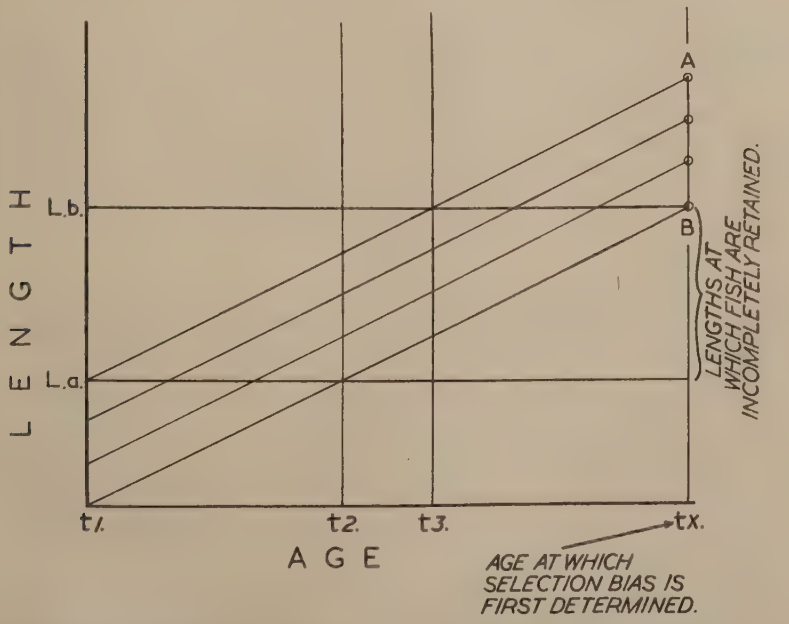

Figure 2. Hypothetical growth curves of four fish during the period of incomplete retention from length L_a cm (0% retention) to length L_b cm (100% retention).

in the year-class reach the length L_b. The expression is $\frac{F\sigma_x^2}{B}$, where F is the instantaneous rate of fishing mortality during the period of incomplete retention, B is the mean rate of growth for the same period and σ_x^2 is the variance of the lengths at age "t_x".

Long Term Effect

In order to determine the effect of selection on the mean length of fish older than "t_x" years, account must be taken of the probable divergence of individual growth curves. Suppose a fish is 4 cm longer than the mean length at age 2 but 8 cm longer at age 5. If the effect of selection is to remove proportionately more of these larger fish, the effect on the mean will become more pronounced as the year-class gets older. Under a reasonable assumption concerning the distribution of sizes the bias increases with age according to the ratio $\frac{\sigma_\varrho}{\sigma_x}$ (see Appendix), where σ_x is the standard deviation at age t_x and σ_ϱ is the standard deviation at some subsequent age t_ϱ. The formula for determining the magnitude of the selection bias at age t_ϱ is then $\frac{F\sigma_x\sigma_\varrho}{B}$.

Application of Formulae to North Sea Haddock

Values of the parameters required for determining the immediate selection bias are given in Table 1 for 70 mm and 80 mm trawl cod-ends and for two areas in the North Sea.

Opposite L_b are given the lengths at which 100% retention occurs for each mesh size. Opposite t_x are given the ages that the year-class has to reach before the smallest individuals are liable to 100% retention. Values of σ_x^2 are taken from Figure 1, which shows the relationship between the "within haul" variance of length at each age for each area. An instantaneous fishing mortality rate of 1·0 is used for all areas (PARRISH and JONES, 1953).

In the last row are given the estimates of the selection bias, corresponding to the different ages in row "t_x".

All the values in the last row of Table 1 relate to different ages, and it is appropriate to use the second formula to determine the magnitude of the effect at any one age. Values of the bias for age 4 (i. e. "ϱ" = 4 years) are given in Table 2.

σ_ϱ is the standard deviation of the lengths at age 4. In the last row is shown the estimated magnitude of the selection bias at age 4. For both sizes of mesh, the effect is greater in the northern North Sea. This is because the growth-rate there is relatively low and so the fish take relatively longer to grow through the incomplete retention phase. For both areas, the effect is greater when an 80 mm cod-end is used. This is because selection by an 80 mm cod-end occurs when the fish are older than when a 70 mm cod-end is used and so their variance is greater and their growth-rate smaller.

Estimates of such a selection effect could have two applications of value. First, it seems probable that an increase in mesh size will have the effect of reducing slightly the mean lengths of the fish at each age. This fact could be used for refining estimates of the effect of changes in mesh size on the yield

Table 1

North Sea Haddock: Steps in the determination of the immediate selection bias for trawl cod-ends of two sizes

Mesh size	70 mm		80 mm	
Area	Northern North Sea	Buchan Deeps	Northern North Sea	Buchan Deeps
L_b (cm)	27	27	30	30
t_x (year)	2·8	2·3	3·8	2·7
B (cm/yr)	5	8	4	7
σ_x^2 (cm^2)	3·8	4·2	5·8	5·4
F	1·0	1·0	1·0	1·0
$\frac{F\sigma_x^2}{B}$ (cm)	0·76	0·52	1·45	0·77

Table 2

North Sea Haddock: Steps in the determination of the selection bias at age 4 years, for two cod-ends

Mesh size	70 mm		80 mm	
Area	Northern North Sea	Buchan Deeps	Northern North Sea	Buchan Deeps
t_x	2·8	2·3	3·8	2·7
B	5	8	4	7
σ_x	1·95	2·05	2·41	2·32
σ_g	2·49	3·00	2·49	3·00
F	1·0	1·0	1·0	1·0
$\frac{F\sigma_x\sigma_g}{B}$	0·97	0·77	1·50	0·99

from a fishery. Secondly, since the selection effect operates by subjecting fast growers to fishing mortality at an earlier age than slow growers, it affords a partial explanation of LEE's phenomenon (LEE, 1912). However, as this effect is confined to the selection phase of the fish's life it can only account for the phenomenon over this period. Since LEE's phenomenon is generally observed over a much wider range of ages, the selection effect can only be advanced as a partial explanation of this phenomenon.

Summary

Mesh selection results in a differential survival rate amongst fish of the same age but of different lengths. This influences the mean length at each age by making it less than it would have been if there had been no "selection effect". The probable magnitude of this effect in the North Sea haddock is calculated and found to vary with the age of the fish, the area from which they come, and the mesh size used in the commercial fishery. Also, it affords a partial explanation of LEE's phenomenon as it accounts for a differential mortality of fast and slow growing fish for at least a short part of their lives.

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Appendix

Four hypothetical growth curves of individual fish are shown in Figure 2. At age t_1, all fish are smaller than L_a cm, the maximum length at which there is no retention by the gear. At age t_x all fish are larger than L_b cm, the minimum length at which there is 100% retention by the gear.

Different fish grow through the period of incomplete retention (L_a to L_b cm) when they are different ages. Fish A for example, grows from L_a to L_b between ages t_1 and t_3. Fish B, on the other hand, does so between ages t_2 and t_x. As a first approximation, it is convenient to assume that the individual growth curves are parallel, so that the time spent in growing from L_a to L_b cm is the same for each fish. The cumulative fishing mortality experienced by each fish when growing from L_a to L_b cm can then be regarded as independent of its relative length.

Consider a year-class that has reached age t_x. The cumulative fishing mortality experienced by each fish is made up of two parts: the first covers the period during which each fish grows from L_a to L_b cm and is the same for all fish: the second covers the period after each fish has reached a length of L_b cm. Suppose a fish has a length of L cm at age t_x. It has grown $(L - L_b)$ cm since it was L_b cm in length and the time required to do this depends on its growth-rate. If the mean rate of growth is constant at B cm/yr, the length of time required to grow $(L - L_b)$ cm is $\frac{(L - L_b)}{B}$ years.

If, during this period, the instantaneous fishing mortality rate is F, the cumulative fishing mortality experienced since the fish was L_b cm in length is given by $\frac{F(L - L_b)}{B}$.

The cumulative total mortality experienced by a fish of length L cm and age t_x years can then be written in the form:
$\frac{F(L - L_b)}{B}$ + fishing mortality over the period of incomplete retention + natural mortality from birth to age t_x, or more briefly $\frac{F(L - L_b)}{B} + K$ where K is a term that is independent of the relative size of the fish.

The probability of survival to age t_x of a fish that is L cm at that age is now given by

$$\exp - \left[\frac{F(L - L_b)}{B} + K\right] \quad \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

Next, suppose that if there were no selection, the frequency distribution of lengths (L) at age t_x would be normal.

i.e. if $P(L)$ is the relative frequency of fish of length L cm

$$P(L) = \frac{1}{\sigma_x \sqrt{2\pi}} \exp - \left[\frac{1}{2\sigma_x^2}(L - L_x)^2\right] \quad \ldots\ldots\ldots\ldots (2)$$

where σ_x^2 is the variance of the lengths and L_x is their mean. However, due to the selection bias, fish of different sizes have different probabilities of survival, given by (1). The expected frequency distribution $P'(L)$ at age t_x is therefore given by the product of (1) and (2). It is:

$$P'(L) = \frac{A}{\sigma_x \sqrt{2\pi}} \exp - \left[\frac{1}{2\sigma_x^2} (L - \bar{L}_x)^2 + \frac{F(L - L_b)}{B} + K \right] \quad \ldots\ (3)$$

where A is chosen so that

$$\int_{-\infty}^{\infty} P'(L)\, dL = 1.$$

After rearranging terms, the expression for $P'(L)$ can be rewritten in the form:

$$P'(L) = \frac{C}{\sigma_x \sqrt{2\pi}} \exp - \frac{1}{2\sigma_x^2} \left[L - \left(\bar{L}_x - \frac{F\sigma_x^2}{B} \right) \right]^2 \quad \ldots\ (4)$$

where C is a term that is independent of length.

The length frequency distribution (4) is still normal with a variance σ_x^2 but the mean is $\left(\bar{L}_x - \frac{F\sigma_x^2}{B} \right)$ instead of $\bar{L}_x$.

The magnitude of the selection bias at age t_x is therefore $\frac{F\sigma_x^2}{B}$.

Long term effect of selection bias

The magnitude of the selection bias at age t_x is given by $\frac{F\sigma_x^2}{B}$. This is a first approximation, based on the assumption that the growth curves of individual fish are parallel during the period of incomplete retention.

To calculate the subsequent magnitude of this bias it is necessary to take account of the fact that the growth curves of individual fish probably diverge. A convenient way of allowing for this is to assume that the deviation from the mean in the length of a fish is proportional to the standard deviation, at all ages.

e. g. Consider a fish that has a length L_x cm when it is t_x years old and a length L_ϱ at some subsequent age t_ϱ. Let the respective mean lengths of the year-class, if there were no selection bias, be $\bar{L}_x$ and $\bar{L}_\varrho$ with standard deviations σ_x and σ_ϱ.

Then this assumption can be written algebraically in the form

$$\frac{L_x - \bar{L}_x}{\sigma_x} = \frac{L_\varrho - \bar{L}_\varrho}{\sigma_\varrho} \quad \ldots\ (5)$$

Suppose a fish has a length L_ϱ cm and is aged t_ϱ years. Its length (L_x) when it was t_x years old is obtained by arranging (5) to give

$$L_x = \frac{\sigma_x}{\sigma_\varrho} \cdot (L_\varrho - \bar{L}_\varrho) + \bar{L}_x \quad \ldots\ (6)$$

The probability of survival to age t_x is given by equation (1).

If (6) is substituted for L in (1) it gives

$$\exp - \left\{ \frac{F}{B} \left[\frac{\sigma_x}{\sigma_\varrho} (L_\varrho - \bar{L}_\varrho) + \bar{L}_x - L_b \right] + K \right\} \quad \ldots\ (7)$$

as the probability of survival to age t_x of a fish that happens to be length L_ϱ cm when it is aged t_ϱ years.

Its subsequent probability of survival from age t_x to age t_ϱ is likely to be independent of its relative length and so the probability of survival to age t_ϱ can be obtained by rewriting (7) with K replaced by K'. This gives:—

$$\exp - \left\{ \frac{F}{B} \left| \frac{\sigma_x}{\sigma_\varrho} (L_\varrho - L_\varrho) + L_x - L_b \right| + K' \right\} \quad \ldots\ldots\ldots \quad (8)$$

Next, let the relative frequency of fish of L_ϱ cm at age t_ϱ in the absence of selection bias be given by

$$P(L_\varrho/t_\varrho) \quad \frac{1}{\sigma_\varrho \sqrt{2\pi}} \exp - \frac{1}{2\sigma_\varrho{}^2} (L_\varrho - L_\varrho)^2 \quad \ldots\ldots\ldots \quad (9)$$

The relative frequency $P'(L_\varrho/t_\varrho)$ when the bias is operating is given by the product of (8) and (9). After rearranging terms this product can be written in the form:

$$P'(L_\varrho/t_\varrho) = \frac{C'}{\sigma_\varrho \sqrt{2\pi}} \exp - \frac{1}{2\sigma_\varrho{}^2} \left| L_\varrho - \left(L_\varrho - F \frac{\sigma_\varrho \sigma_x}{B} \right) \right|^2 \quad \ldots\ldots \quad (11)$$

The selection bias at age t_ϱ is therefore given by $\frac{F \sigma_\varrho \sigma_x}{B}$.

A Note on the Dependence of Catches on Temperature and Wind in the Buchan Pre-Spawning Herring Fishery

By

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Craig (1957) has shown an association between herring drifter catches and the rate of rise of surface temperature during the Buchan pre-spawning fishery. It can also be shown that there is an association of catch with the wind conditions, and that these two factors, taken together, account for a large part of the variability in catch of the fish of four years of age or more.

(1). The Buchan fishery and the recent changes in its character have been described by Parrish and Craig (1957). In Table 1 are shown the mean catch per arrival of herring of four years of age and older in the period May-July, 1930–57, excluding the war years.

(2). Surface temperature anomalies for the area "F" in the north-western North Sea in these years have been taken from records prepared by Smed (1946–1958). From these records the figures A of Table 1 have been derived as follows:—

$$A = \frac{\text{anomaly May} + \text{anomaly June} + \text{anomaly July}}{3} - \text{anomaly March}$$

Thus A is a measure of the rate of increase of surface temperature during the early summer. Low values of A suggest that vertical mixing has been relatively strong, and vice versa.

(3). Wind components for the northern North Sea have been taken from records prepared by the German Hydrographic Institute (Dietrich, *et al.* 1952, and subsequent routine records). From these components the values of S in Table 1 have been derived. S is the wind component from the south in metres per second, averaged over April, May, June, and July.

(4). Simple regressions.

The data of Table 1 have been analysed by Mr. J. A. Pope. He finds that:—

(a) The correlation coefficient of C on A is $-0{\cdot}48$ (significant at 5% level).

(b) The correlation coefficient of C on S is $+0{\cdot}42$ (not quite significant at 5% level).

Table 1

Average catch per arrival of herring of four years old and more in the Buchan pre-spawning fishery, compared with rate of rise of surface temperature, and the wind component from the south during the fishery

	Average catch per arrival in crans (*C*)	Change of surface temperature anomaly from March to May, June, July in tenth °C (*A*)	Wind component from south in m/sec. (*S*)
1930	10·5	5	0·80
31	10·4	4	1·67
32	10·6	−4	−0·22
33	5·9	15	−0·47
34	9·2	0	0·25
35	10·5	−3	−1·57
36	8·4	8	−0·97
37	8·5	8	−0·17
38	13·6	−9	−0·50
39	6·8	−4	0·12
1947	9·3	14	1·05
48	10·4	−5	0·37
49	5·6	3	−0·67
50	12·4	−2	0·22
51	12·2	−1	−0·40
52	18·2	−2	0·97
53	13.9	−1	0·50
54	8·9	6	0·17
55	7·7	6	−1·15
56	9·9	1	−0·70
57	5·4	1	−1·15

These basic data are illustrated in Figures 1 and 2.

(5). Multiple regressions.

Since the above findings appear to justify closer analysis, a partial correlation was tested, i. e., the influence of S was eliminated when testing for A, and the influence of A was eliminated when testing for S, with the following result:—

(a) The correlation coefficient of C on A (S eliminated) is $-0{\cdot}57$ (significant at 1% level).

(b) The correlation coefficient of C on S (A eliminated) is $+0{\cdot}52$ (significant at 2% level).

(c) The best fit to the multiple regression of C on A and S is $C = 10{\cdot}6 - 0{\cdot}257A + 1{\cdot}71S$.

Thus rapid warming of the surface water, and prevalence of winds from the north are associated with a reduction in the catch of herring of four years old and older in this fishery, and vice versa. We might say that these factors influence the "availability" of the fish, where this term should be taken in its widest sense to include differences in behaviour, distribution, or aggregation which might affect the catch obtained from a year-class of given strength. At this stage the writer does not postulate any particular mechanism by which the changes in availability are caused.

The actual values of catch must necessarily depend on year-class strengths as well as on "availability", and a most useful check on the above relationships is provided by an examination of apparent survival rates, which are independent of the strengths of the year-classes. This examination is made below.

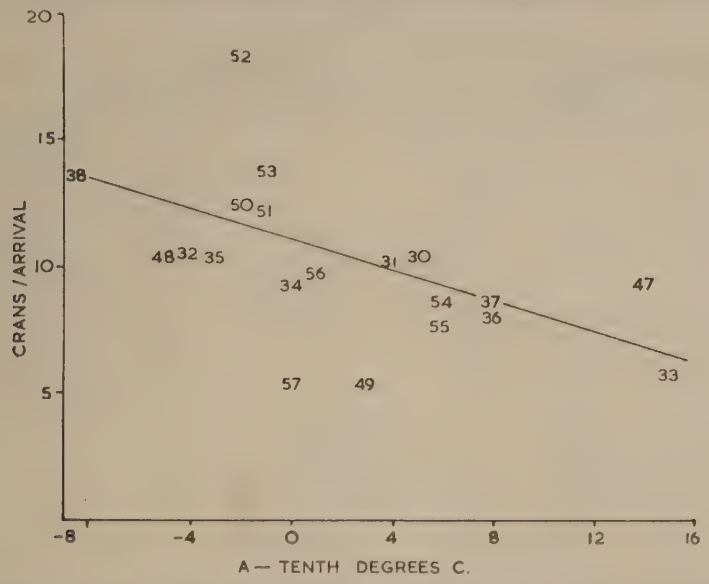

Figure 1. Average catch per arrival of herring of four years old and more in the Buchan pre-spawning fishery, plotted against the rise (*A*) of surface temperature anomaly during the corresponding season. The point for 1930 is represented by the figure 30 and so on.

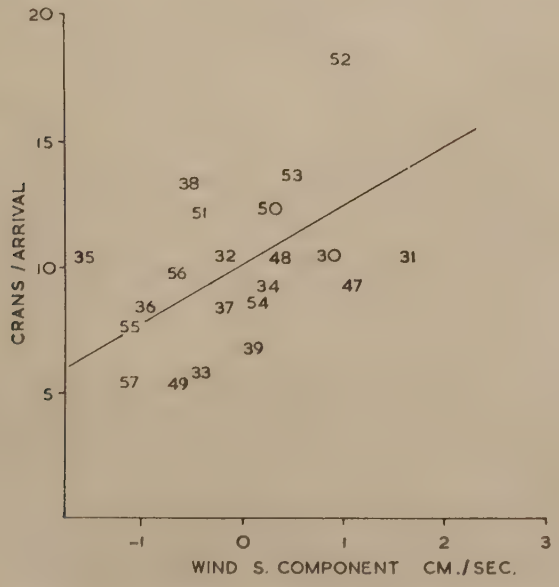

Figure 2. Average catch per arrival of herring of four years old and more in the Buchan pre-spawning fishery, plotted against the wind component from the south (*S*) during the corresponding season. The point for 1930 is represented by the figure 30 and so on.

Table 2

Expected survival rate (%) and observed survival rate (%) among herring of four years old and more in the Buchan pre-spawning fishery

	Expected survival rate %	Observed survival rate %		Expected survival rate %	Observed survival rate %
1930–31	63	57	1947–48	86	73
31–32	49	31	48–49	38	34
32–33	29	21	49–50	71	120
33–34	101	107	50–51	48	73
34–35	43	39	51–52	67	111
35–36	42	43	52–53	50	41
36–37	65	74	53–54	43	33
37–38	79	64	54–55	40	29
38–39	53	28	55–56	69	34
			56–57	49	13

(6). Survival rates.
The observed apparent survival rate is taken to be:—

$$100\% \cdot \frac{\text{catch per arrival of fish of 5 years old or more in year 2}}{\text{catch per arrival of fish of 4 years old or more in year 1}}$$

To provide a figure for comparison with this we first calculate an "expected" catch for each year, using the regression of (c) above. We then obtain an expected apparent survival rate in the form:—

$$54\% \cdot \frac{\text{expected catch year 2}}{\text{expected catch year 1}}$$

(The value 54% is the mean observed survival rate for the whole period considered.)

The values of observed and expected apparent survival rates are given in Table 2 and Figure 3. It is immediately apparent that there is a significant correlation. Figure 3, however, tells more than this. For the first fourteen pairs of years, the relationship is very close indeed. Then there follow 1949–50, 1950–51, and 1951–52 in which the observed survival is considerably higher than the expected. The next three pairs correspond with expectation, and then follow 1955–56 and 1956–57 when the observed survival rate fell below expectation.

(7). Comparison of early with recent period.

(a) For the period 1930–1949 the correlation coefficient between observed and expected apparent survival rate was 0·92 (significant at 0·01% level) and so *changes in survival rate in this period are largely accounted for by known changes in wind and temperature conditions during the fishing season.*

(b) For the recent period we note that in 1949–1952 the survival rates were all much higher than can be accounted for by these known factors; again, in the period 1955–57, the survival rates were well below expectation. This can be seen in Figure 4.

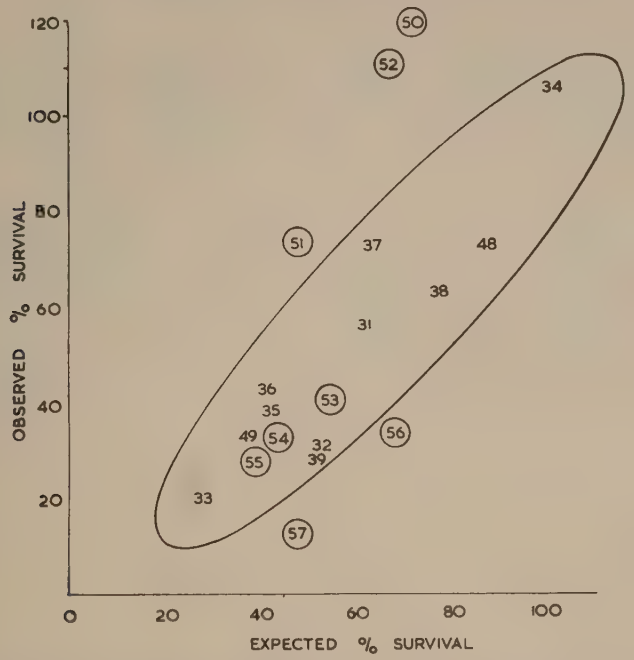

Figure 3. Actual survival rate of herring of four years old and more in the Buchan pre-spawning fishery, plotted against the "expected" survival rate deduced from the observed regressions. The point for 1930–31 is represented by the figure 31 and so on.

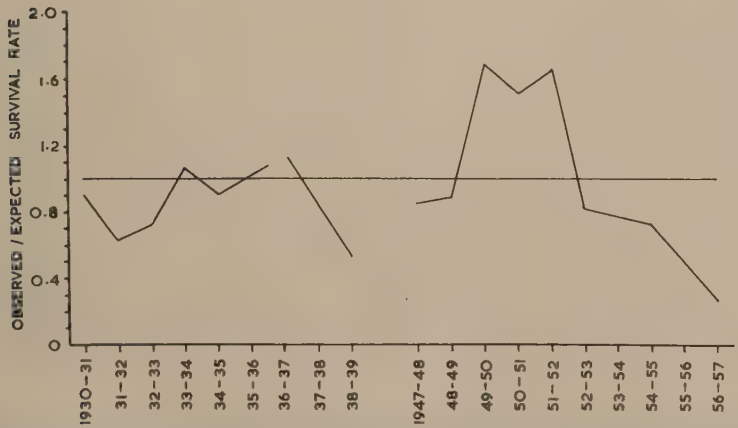

Figure 4. The ratio of observed to expected survival rates for herring of four years old and more in the Buchan pre-spawning herring (see text). Observed values are much below expectation for the pair of years 1938–39 and in 1955–56 and 1956–57. They were much above expectation in 1949–50, 1950–51, and 1951–52.

Summary

Availability of herring of four years old and older in the Buchan prespawning fishery is shown to be related to wind and temperature. From 1930 to 1949 these factors account for most of the variations, but subsequent to 1949 they only account partially for the observed variations.

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Some Observations on the Body Proportions of North Sea Autumn Spawning Herring

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Introduction

One of the most important aims in the studies known generally as "racial investigations" is to determine the number of self-contained dynamic groups within the range of distribution of a species, to delimit the distribution of each, and to measure the degree of inter-mixing between them. The identification and description of these "unit-stocks" is of fundamental importance in population studies, especially for interpreting changes in the yields from the fisheries and in gauging the effects of possible conservation measures. For few species is the importance of these investigations greater than for the herring of the North Atlantic, especially the North Sea, which has been the subject of intensive scientific study for many years.

That the total herring resource of the North-East Atlantic does not constitute a single homogeneous population was established by the classical researches initiated by HEINCKE (1898) and subsequent workers. The long-term study of physiological and morphological characters of herring caught in different regions of the North Atlantic has shown that a major subdivision can be made between a "winter-spring" spawning group, with a spawning season between February and April, and a "summer-autumn" spawning group, spawning between August and December. These major groups are generally regarded by herring biologists as distinct spawning groups between which inter-breeding is negligible or absent and which warrant subspecific or specific taxonomic status (KREFFT, 1955; BLAXTER, 1958).

These studies have also provided evidence of further possible subdivisions within each of these groups, and their identification and delimitation has been the subject of intensive research by herring workers for many years. A major group which has received detailed attention is the "summer-autumn" spawning group inhabiting the North Sea, on which the major North Sea herring fisheries are principally based.

Spawning by this group takes place between August and December in three main localities. These are:—

(1) the coastal and offshore banks off the Scottish east coast in August and September;
(2) the slopes of the Dogger Bank in late September and October, and
(3) the eastern regions of the English Channel and neighbouring banks in November and December.

Spawning has also been reported in other localities in some years (e. g., the Jutland Bank) but these localities are of minor importance as spawning centres.

The results of long-term investigations have shown convincingly that there is some, if not complete, segregation between the groups of herring spawning in these three localities but there is still doubt as to the extent of the subdivision. For example, CUSHING (1955) concludes that the "summer-autumn" spawners of the North Sea can be subdivided into two major spawning groups, the "Bank" group, which spawn on and to the north of the Dogger Bank and the "Downs" group which spawn in the eastern Channel and neighbouring localities, while ZIJLSTRA (1958) advocates a breakdown of the population into a greater number of spawning groups. Thus, this subject is still under intensive investigation; characters which hitherto have received little or no attention are being investigated, and techniques for observing the movements of herring are being used, to provide a more detailed picture of the migrations to and from the spawning grounds.

Amongst the characters which have received only slight attention by European herring workers are the relative dimensions of the different parts of the body. Although some scattered observations of these characters were made by early European herring workers, they have not been subject to systematic study in the North Sea herring "racial" investigations. This paper deals with the results obtained from a preliminary study of these characters among herring spawning in the northern (Banks) and southern regions (Downs) of the North Sea between July and November 1956, with a view to revealing any differences between the body proportions in the two spawning groups and assessing the possible value of these characters in herring "racial" studies in these regions. The body dimensions chosen for study were the length of the head and the length of the body, measured as both "fork" and total length.

Material and Methods

The material consisted of spawners (maturity stage VI) from the Scottish east coast (Buchan) spawning grounds in August and September, which belong to the "Bank" group, and pre-spawners of the "Downs" group, principally of maturity stage V from the East Anglian drift-net fishing grounds. The Scottish sample consisted of 243 fish (142 males and 101 females) ranging in age between

2 and 16 years[1]) and total length between 25 and 31 cm; the East Anglian material comprised 288 fish (160 males and 128 females) between 2 and 9 years of age and 24–30 cm total length.

The fish were selected at random from the routine samples handled each day in the laboratory, and measurements of total length, fork length, and head length were made on each. The sex of each fish was also determined and scales were taken for age analysis.

Total length was measured, using a standard measuring board, from the tip of the snout to the tip of the longest ray of the lower lobe of the caudal fin with the lobes spread. The distance between this point and the shortest caudal fin ray was then measured with dividers. This gave a measure of fork length by subtraction from the total length. The head length was measured from the tip of the snout to the posterior pigmented end of the gill cover. Readings of this dimension were taken with a ruler held horizontally along the head. All lengths were measured to the nearest millimetre[2]).

Results

A preliminary analysis was made of the head length H/total length L, and head length/fork length F ratios for each sex and for each length and age category in each group of spawners. The frequency distributions of these ratios for each sex, age, and centimetre length group are given in Tables 1–8, which, for convenience, have been put at the end of the paper, and of the head length/total length ratios for sex and age categories in Figures 1 and 2.

This preliminary study of the material revealed some important similarities and differences between the body proportions of the different sex, length, and age-groups within each spawning group, and between spawning groups. The most striking and relevant of these were as follows:—

(1) For each spawning group, the forms of the distributions of head length/total length and head length/fork length ratios were approximately the same. Subsequent analyses were therefore confined to the head length and total length data.

(2) While amongst the younger, smaller fish (2–3 winter-rings), the ratios in the two spawning groups were similar, those of the larger, older fish were higher for the Scottish than for the East Anglian fish.

(3) The difference in the body proportions between sex, age, and length categories within spawning groups were generally smaller than between spawning groups. However, in the East Anglian material the ratios for both sexes tended to be higher for the younger, smaller fish than for the older, larger ones. In the Scottish material, on the other hand, the older larger fish tended to have the larger ratios.

Strictly, a direct comparison of ratios of two correlated dimensions of this type is only valid if the relationship between them is an exactly proportional one of the form $H = bL$. If it is of the form $H = a + bL$, the H/L ratios will be a function of L and differences between the mean ratios of groups may be due to differences in the mean values of L which may account for the apparent

[1] Measured as number of winter-rings on the scales.

[2] For convenience, centimetre grouping intervals were used. Measurements from x to $x + 0{\cdot}9$ cm were classed as x where x is a whole number.

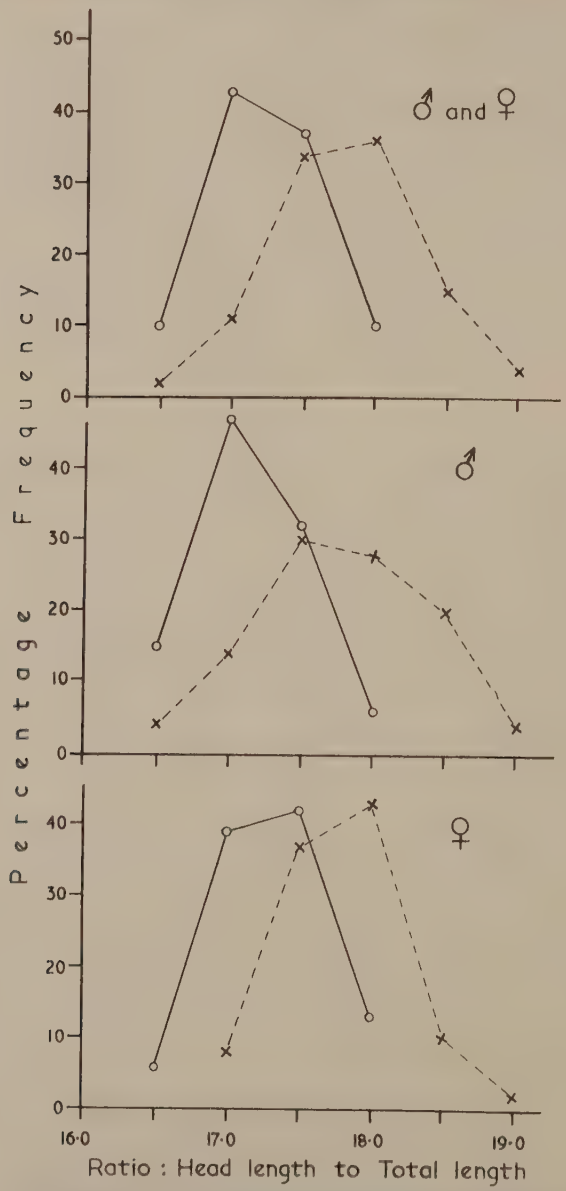

Figure 1. Percentage frequency distributions of head length/total length ratios for Scottish (×– – –×) and East Anglian (○——○) samples.
5 and older age-groups combined.

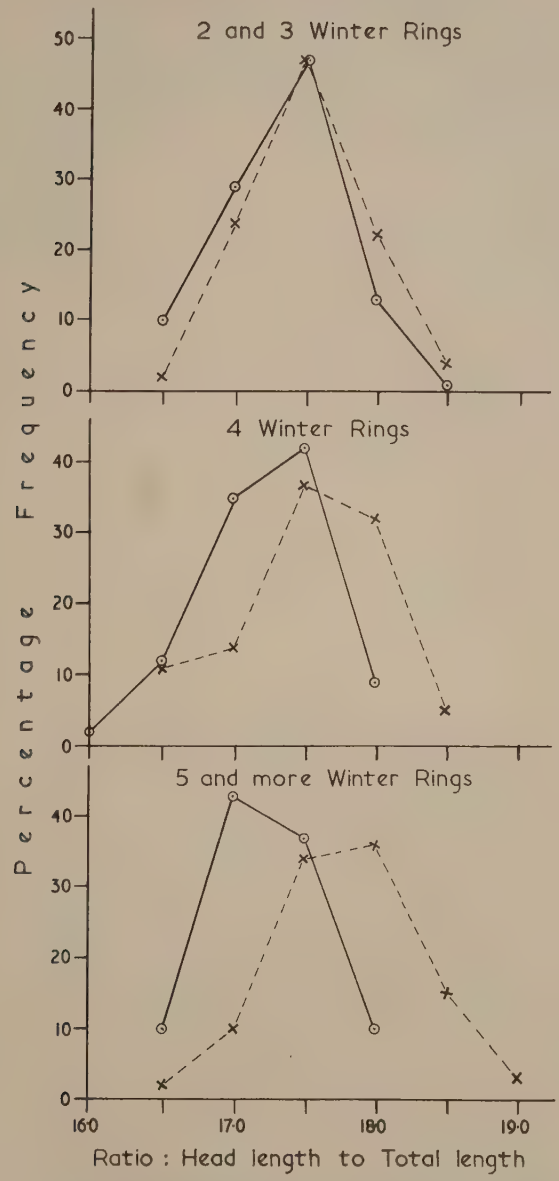

Figure 2. Percentage frequency distributions of head length/total length ratios for age categories in the Scottish (×– – –×) and East Anglian (⊙——⊙) samples. Sexes combined.

change in the body proportion with age. Therefore, confirmation of the results obtained from this preliminary analysis was sought by a more detailed analysis of the data, using two other statistical methods. These were:—

(a) Covariance analysis (Snedecor, 1956; Mottley, 1941). The regression of H on L was determined for each sex and age category in each spawning group, and the slope and intercept parameters for the groups were compared by covariance analysis.

(b) Multivariate analysis (Wilks, 1932; Bartlett, 1947). This method differs from the analysis of covariance in treating both variates as of equal "standing". This analysis was carried out by Mr. J. A. Pope, and the statistical features of the two methods are given in the Appendix.

The results of this analysis provided confirmation of the main provisional conclusions drawn from the simple analysis of the head length/total length ratios. Thus a significant difference was established between the body proportions of the two spawning groups, the Scottish spawners having, on average, a significantly greater head length than the East Anglian spawners, after allowing for differences in total length between the groups. This difference was greater amongst the older, larger fish than the younger, smaller ones. Differences were also detected between the sexes in both areas. These were greatest in the Scottish material in which the head length/total length regressions were significantly different between sexes in all age-groups. The relationship for males changed significantly with age. The sex differences in the East Anglian material were less marked.

Discussion

This preliminary analysis of a limited number of data from two groups of spawners in the North Sea in only one year suggests that a longer term and more intensive study of body proportions of spawners from the main spawning grounds in the North Sea might be of value, along with other criteria, in herring "racial" investigations. The results indicate clearly that the spawners in the northern and southern regions of the North Sea possessed significant relative growth differences, which were most marked in the fully recruited age-groups. This is shown clearly in Appendix Table I and by the distributions of head length/total length ratios for the fish with five and more rings in Figure 2, which exhibit a small degree of overlap. These observations are consistent with the generally accepted view that the interchange of spawners between the northern and southern North Sea spawning areas is small.

The interpretation of the difference in the body proportions of the Scottish male spawners between the younger and older age-groups, is not clear. It might be due to either a difference in relative growth between different year-classes of a unit stock, or a difference in the origin of all or a proportion of the younger and older spawners in this area. A more comprehensive analysis of the body proportions of specific year-classes at successive ages in the spawning fishery is required to shed further light on this phenomenon. It is possible, however, that these age differences were due, in part at least, to a change in the "racial" composition of the male spawners on this ground.

Summary

Observations were made of the head length and the total and fork lengths of samples of herring spawning in the north-western North Sea off the Scottish east coast in August and September, and of pre-spawners (stage V) from the Southern Bight, caught off the East Anglian coast in October and November 1956.

Comparisons of these dimensions were made using standard statistical techniques (see Appendix) and the following results were observed:—

(1) The relation between head length and total length was significantly different between the spawning groups in the two areas, especially amongst the older age-groups. The Scottish spawners had on average the longer heads.

(2) Significant differences were detected between the head length/total length relationship for the two sexes in each group. This difference was dependent on age in all groups except the Scottish females.

The conclusion is drawn that a longer term and more intensive study of the body proportions of spawners on each of the major North Sea spawning grounds might be of value in North Sea "racial" investigations.

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Table 1

Distribution of the head length/total length and head length/fork length ratios for successive length categories

East Anglia, male herring

Total length (cm)	$\frac{H \cdot 100}{L}$ 16·0	16·5	17·0	17·5	18·0	18·5	$\frac{H \cdot 100}{F}$ 18·0	18·5	19·0	19·5	20·0	20·5	Total
24	–	–	–	1	–	–	–	–	–	1	–	–	1
25	–	1	5	6	4	–	–	1	3	7	4	1	16
26	1	10	12	22	8	3	2	9	15	17	8	5	56
27	–	2	14	21	4	1	–	6	13	17	5	1	42
28	–	3	16	8	2	–	1	4	17	5	2	–	29
29	–	4	3	2	–	–	2	2	3	2	–	–	9
30	–	1	2	3	1	–	–	2	2	2	1	–	7
Total	1	21	52	63	19	4	5	24	53	51	20	7	160

Table 2

Distribution of the head length/total length and head length/fork length ratios for successive length categories

East Anglia, female herring

Total length (cm)	$\frac{H \cdot 100}{L}$ 16·0	16·5	17·0	17·5	18·0	18·5	$\frac{H \cdot 100}{F}$ 18·0	18·5	19·0	19·5	20·0	Total
25	–	–	3	6	2	–	–	–	4	4	3	11
26	–	3	8	23	2	1	2	1	7	22	5	37
27	1	2	15	15	4	–	1	4	15	12	5	37
28	–	1	11	8	3	–	–	4	6	10	3	23
29	–	1	5	10	–	–	–	1	7	7	1	16
30	–	1	2	–	–	–	–	1	2	–	–	3
Total	1	8	44	62	11	1	3	11	41	55	17	127

Table 3

Distribution of the head length/total length and head length/fork length ratios in age categories

East Anglia, male herring

Age (rings)	$\frac{H \cdot 100}{L}$ 16·0	16·5	17·0	17·5	18·0	18·5	$\frac{H \cdot 100}{F}$ 18·0	18·5	19·0	19·5	20·0	20·5	Total
2	–	4	4	6	1	–	1	3	2	8	1	–	15
3	–	4	12	23	10	1	–	5	14	17	10	4	50
4	1	8	19	19	6	3	2	12	19	13	7	3	56
5	–	4	10	7	1	–	1	3	10	7	1	–	22
6	–	–	4	2	1	–	–	–	5	1	1	–	7
7	–	1	2	1	–	–	1	1	2	–	–	–	4
8	–	–	–	–	–	–	–	–	–	–	–	–	–
9	–	–	–	1	–	–	–	–	–	1	–	–	1
Total	1	21	51	59	19	4	5	24	52	47	20	7	155

Table 4

Distribution of the head length/total length and head length/fork length ratios in age categories

East Anglia, female herring

Age (rings)	$\frac{H \cdot 100}{L}$						$\frac{H \cdot 100}{F}$						
	16·0	16·5	17·0	17·5	18·0	18·5	18·0	18·5	19·0	19·5	20·0	20·5	Total
2	–	1	1	2	2	–	1	–	1	2	2	–	6
3	–	3	17	24	2	1	1	4	16	20	5	1	47
4	1	2	11	19	1	–	1	5	7	18	2	1	34
5	–	2	8	10	3	–	–	2	8	10	3	–	23
6	–	–	4	4	1	–	–	–	5	3	1	–	9
7	–	–	–	1	–	–	–	–	–	1	–	–	1
8	–	–	1	–	1	–	–	–	1	–	1	–	2
9	–	–	1	–	–	–	–	–	1	–	–	–	1
Total	1	8	43	60	10	1	3	11	39	54	14	2	123

Table 5

Distribution of the head length/total length and head length/fork length ratios for successive length categories

Buchan Area, male herring

Total length	$\frac{H \cdot 100}{L}$						$\frac{H \cdot 100}{F}$							
	16·5	17·0	17·5	18·0	18·5	19·0	18·0	18·5	19·0	19.5	20·0	20·5	21·0	Total
25	–	–	2	1	1	–	–	–	2	–	1	–	1	4
26	–	–	10	3	1	–	–	–	1	9	3	1	–	14
27	–	5	14	8	1	–	–	1	7	13	6	1	–	28
28	4	8	16	13	3	–	1	6	9	13	13	2	–	44
29	2	3	8	4	3	–	–	2	5	7	3	3	–	20
30	1	5	7	9	5	1	–	2	6	5	7	7	1	28
31	–	–	2	–	1	1	–	–	–	1	1	1	1	4
Total .	7	21	59	38	15	2	1	11	30	48	34	15	3	142

Table 6

Distribution of the head length/total length and head length/fork length ratios for successive length categories

Buchan Area, female herring

Total length	$\frac{H \cdot 100}{L}$						$\frac{H \cdot 100}{F}$							
	16·5	17·0	17·5	18·0	18·5	19·0	18·5	19·0	19·5	20·0	20·5	21·0	21·5	Total
26	–	–	1	–	–	–	–	–	1	–	–	–	–	1
27	1	2	3	3	1	–	1	3	3	3	–	–	–	10
28	1	9	5	4	–	–	3	7	7	2	–	–	–	19
29	–	1	8	8	1	–	–	3	6	7	2	–	–	18
30	–	5	15	13	3	1	–	8	12	13	3	–	1	37
31	–	2	4	8	2	–	–	2	7	6	1	–	–	16
Total .	2	19	36	36	7	1	4	23	36	31	6	–	1	101

Table 7

Distribution of the head length/total length and head length/fork length ratios in age categories

Buchan Area, male herring

Age (rings)	$\frac{H \cdot 100}{L}$						$\frac{H \cdot 100}{F}$							
	16·5	17·0	17·5	18·0	18·5	19·0	18·0	18·5	19·0	19·5	20·0	20·5	21·0	Total
2	–	2	7	1	2	–	–	1	3	5	1	1	1	12
3	2	9	27	13	2	–	–	4	13	23	11	2	–	53
4	3	3	10	10	1	–	1	2	6	9	8	1	–	27
5	1	4	7	4	2	–	–	1	5	5	4	3	–	18
6	1	1	4	–	1	–	–	2	1	2	2	–	–	7
7	–	–	3	3	1	–	–	–	1	3	2	1	–	7
8	–	–	–	3	1	–	–	–	–	–	3	1	–	4
9	–	1	–	1	–	1	–	–	1	–	1	–	1	3
10	–	–	–	–	2	1	–	–	–	–	–	2	1	3
11	–	–	1	2	–	–	–	–	–	1	2	–	–	3
12	–	1	–	–	3	–	–	1	–	–	–	3	–	4
13	–	–	–	–	–	–	–	–	–	–	–	–	–	–
14	–	–	–	–	–	–	–	–	–	–	–	–	–	–
15	–	–	–	–	–	–	–	–	–	–	–	–	–	–
16	–	–	–	1	–	–	–	–	–	–	–	1	–	1
Total .	7	21	59	38	15	2	1	11	30	48	34	15	3	142

Table 8

Distribution of the head length/total length and head length/fork length ratios in age categories

Buchan Area, female herring

Age (rings)	$\frac{H \cdot 100}{L}$						$\frac{H \cdot 100}{F}$							
	16·5	17·0	17·5	18·0	18·5	19·0	18·5	19·0	19·5	20·0	20·5	21·0	21·5	Total
2	–	1	–	–	–	–	–	1	–	–	–	–	–	1
3	–	10	8	6	–	–	2	9	10	3	–	–	–	24
4	2	3	6	4	1	–	2	4	5	5	–	–	–	16
5	–	2	7	6	–	–	–	3	6	5	1	–	–	15
6	–	–	5	6	1	–	–	2	3	6	1	–	–	12
7	–	2	3	3	2	–	–	2	4	3	1	–	–	10
8	–	–	4	6	–	–	–	1	3	6	–	–	–	10
9	–	1	3	4	3	–	–	1	4	3	3	–	–	11
10	–	–	–	–	–	–	–	–	–	–	–	–	–	–
11	–	–	–	1	–	–	–	–	1	–	–	–	–	1
12	–	–	–	–	–	–	–	–	–	–	–	–	–	–
13	–	–	–	–	–	1	–	–	–	–	–	–	1	1
Total .	2	19	36	36	7	1	4	23	36	31	6	–	1	101

Appendix

The analysis of differences in the ratios of head length to total length in two or more groups depends on the form of the relationship between the measurements. As pointed out above the use of ratios of the form H/L is likely to be dangerous if the relationship is not strictly proportional. The most widely used though not the only relationship between two variates is the regression relationship. If two variates, which for convenience we will here call H and L, are both distributed according to the normal bivariate frequency law then for any specified value of one of them, $L = L_0$ say, the values of the other H are distributed according to the normal uni-variate frequency law. The mean value of this conditional frequency distribution of H depends on the value at which L is fixed and as L varies the mean moves along a straight line whose equation may be denoted by

$$\hat{H} = \alpha + \beta L \qquad (1)$$

This equation is called the regression of H on L. It is to be used to give the average value of H for a given value of L. It is not necessary for the linearity of the regression that H and L be both normally distributed but normality will usually be assumed at some point in order to allow tests of significance.

The computations involved in estimating (1) from a random sample of pairs of observations on H and L are well known and may be found in any standard statistical textbook (e. g., SNEDECOR, 1956). Regression lines in two or more groups may be compared by a simple method of analysis described fully by FISHER (1947).

Comparisons between the Scottish and East Anglian regressions were made for the two sexes separately and for three age-groups, viz., 2–3 years, 4–5 years, and 6 years and older (measured as winter scale-rings). These six analyses showed that with only one exception the average head length of Scottish herring was significantly greater than the average head length of East Anglian herring. The exception was in the 2–3 year-old females which showed no significant difference between average head lengths. The average head length differences adjusted for differences in total length, together with their standard errors are shown in Table 1.

Table 1

Average head length differences (mm) between Scottish and East Anglian herring adjusted for total length differences

Age in years	Male	Female
2–3	0·08 ± 0·025	0·05 ± 0·053
4–5	0·16 ± 0·031	0·12 ± 0·044
≥6	0·17 ± 0·063	0·18 ± 0·065

Thus, the differences in head length between Scottish and East Anglian herring increase with age.

Having in this way established differences between the two spawning groups at each age further analysis may be conveniently confined to studying changes in body dimensions within the spawning groups. Regression analysis is not

appropriate here for it is really the homogeneity of the biological relationship between H and L which we wish to test. This form of relationship has received the name of the line of organic correlation and has been discussed from a statistical standpoint by, among others, TEISSIER (1948) and KERMACK and HALDANE (1950). It is not at all certain, however, that the line suggested by these authors is the best one nor does an efficient method of comparing such lines or similar ones appear to exist.

One point which lies on the line corresponding to the biological relationship is the point with co-ordinates H, L. We may accordingly proceed here by analysing differences in the pairs of means in each sex and age class for the two spawning groups. The analysis of dependent variates such as H and L falls within the realm of multivariate analysis and our problem may be handled by a bivariate analysis of variance.

In an ordinary univariate analysis of variance the significance of differences between mean values in a particular set of classes is tested using the criterion

$$\frac{\text{mean square between classes}}{\text{mean square for error}}$$

An alternative test is provided by the criterion

$$\frac{\text{sum of squares for error}}{\text{sum of squares for error} + \text{sum of squares for classes}}$$

WILKS (1932) has shown that this second criterion may be generalized to any number of variates the criterion being

$$\Lambda = \frac{|\mathbf{E}|}{|\mathbf{E}+\mathbf{C}|}$$

where $\mathbf{E}$ is the matrix of error sums of squares and products of all variates, $\mathbf{C}$ the matrix of between classes sums of squares and products of all variates and $|\mathbf{E}|$ and $|\mathbf{E}+\mathbf{C}|$ being determinants of the matrices $\mathbf{E}$ and $\mathbf{E}+\mathbf{C}$. For the analyses required here the exact distribution of Λ is known.

In the analysis of the data the 2×2 matrix of total sums of squares and products was first split up into component matrices of orthogonal sums of squares and products as follows:—

	d. f.	*S. of P. matrix*
Between ages (eliminating sex)	2	**A**
Between sexes (eliminating ages).....	1	**S**
Interaction	2	**H**
Error		**E**

Significant sex and age differences were detected, differences between ages being expected as both L and H increase naturally with age. In our case, however, it is the form of the change in mean levels with age which is of interest. In particular we wish to know whether the mean values of L and those of H follow a linear trend with age (t). In such a case we have

$$L = a_1 + b_1 t, \qquad H = a_2 + b_2 t$$

$$\text{and} \qquad \frac{L - a_1}{b_1} = \frac{H - a_2}{b_2}$$

i. e., L and H are linearly related.

Because of the difference between sexes this regression analysis was carried out separately for the two sexes. The results showed that deviations from linearity were significant in the case of males but not for females. This suggests that while the relationship between H and L is constant irrespective of age in the case of females this is not so for males.

A similar analysis of the East Anglian data showed that for neither sex could the relationship between H and L be regarded as linear over the whole age range.

Observations on the Size and Numbers of Herring Taken by the Herring Trawl

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Introduction

HJORT (1912) and EHRENBAUM (1925) have said that the catches of the bottom herring trawl tend to increase in the hours of daylight; JENKINS (1927), however, states that the time at which the largest catches are made differs according to the ground and season. LUCAS (1936) showed from an analysis of the herring catches made from commercial herring trawlers landing at Hull and North Shields, that there was a variation in the length of herring taken during the day. He points out that the proportion of large herring in the catches was greater by night than by day, and suggests that the small and possibly immature herring were not caught at night because they execute a more extensive upward migration at night than the larger fish. Earlier, FULTON (1922) had said that the herring in the catch were longer by day than by night.

Thus, there is apparently disagreement of the evidence both on the diurnal variation in numbers and on the diurnal variation in length, and the purpose of this paper is to attempt to resolve these disagreements.

Methods

Four cruises of the R/V "Sir Lancelot" (XIII, XIV, XV, and XVI 1956) were devoted to collecting data on herring trawling in August, September, and October 1956 on various North Sea trawling grounds. Hauls were taken for a standard time (1 hour) at all hours from dawn to dusk.

In September 1957, a cruise was made on R/V "Anton Dohrn" (with the kind permission of Professor BÜCKMANN). For two days on the Dogger, hauls were made for a standard time (half an hour) at all times of day and night.

Samples of fish were examined for length and stage of maturity on HJORT's scale.

Table 1

Numbers of herring caught per standard haul in each 4-hour period, and percentage of the average number per standard haul for the day

2400–0359 hs		0400–0759 hs		0800–1159 hs		1200–1559 hs		1600–1959 hs		2000–2359 hs	
No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
221	74·0	31	4·7	147	22·1	1274	191·6	987	148·4	101	33·8
1980	124·5	156	31·8	888	133·5	350	71·2	190	38·7	213	71·3
71	4·5	284	57·8	1274	191·6	700	142·5	1400	285·0	51	17·1
		72	191·5	150	30·5	14	37·2	720	117·2	2454	154·4
		500	111·8	700	142·5	265	43·1	472	76·8		
		280	62·6	1000	162·8	410	91·6	0	0·0		
		232	16·7	54	143·6	235	52·5	810	181·0		
		480	122·0	48	127·7	1000	72·0	4700	338·5		
		220	45·0	280	62·6	1200	86·4	2	0·5		
		180	36·8	450	100·6	600	152·4	111	22·7		
		375	50·6	500	36·0	1400	286·5	700	177·8		
		10	19·0	700	50·4	1428	292·2	475	159·0		
		28	53·2	186	47·3	1300	435·1	254	85·0		
		84	28·1	33	6·8	173	30·8	113	20·1		
		223	74·6	49	10·0	3630	228·4	453	28·5		
		2288	144·0	1000	134·8			2826	177·8		
		776	48·8	850	114·6			197	12·4		
				28	53·2						
				120	227·9						
				66	22·1						
				1400	249·1						
				1215	76·5						
Mean %	67·7		64·6		97·6		147·6		116·8		69·1

Results

The results may be grouped under three heads, the diurnal variation in numbers caught, the diurnal variation in length, and the diurnal variation in the proportions of different maturity stages.

Tables 3, 4, and 5 are, for convenience, placed at the end of the paper. Table 3 gives the times, dates, and positions of hauls on Cruises XIII, XIV, XV, and XVI of "Sir Lancelot", 1956, and of the cruise of "Anton Dohrn", 1957; the numbers of fish per hour ("Sir Lancelot") or per half hour ("Anton Dohrn"), and the mean lengths of each sample are also given. Table 4 gives the percentage length distribution caught at each station and Table 5 gives the numbers of fish caught, and their mean lengths, for immature, spent, and full fish.

(a) The diurnal variation in numbers

The day was split into four-hour periods:— 2400 hours–0359 hours; 0400 hours–0759 hours; 0800 hours–1159 hours; 1200 hours–1559 hours; 1600 hours–1959 hours; 2000 hours–2359 hours. The numbers caught in each haul were expressed as a percentage of the average numbers caught per standard haul on that day, and these percentages were averaged for each four-hour period. The grouping of numbers caught and derivation of percentages is shown in Table 1. The trend of the average percentages for each four-hour period throughout the day is shown in Figure 1. There is a two-fold variation in proportion throughout the day, reaching a peak between 1200 and 1600 hours.

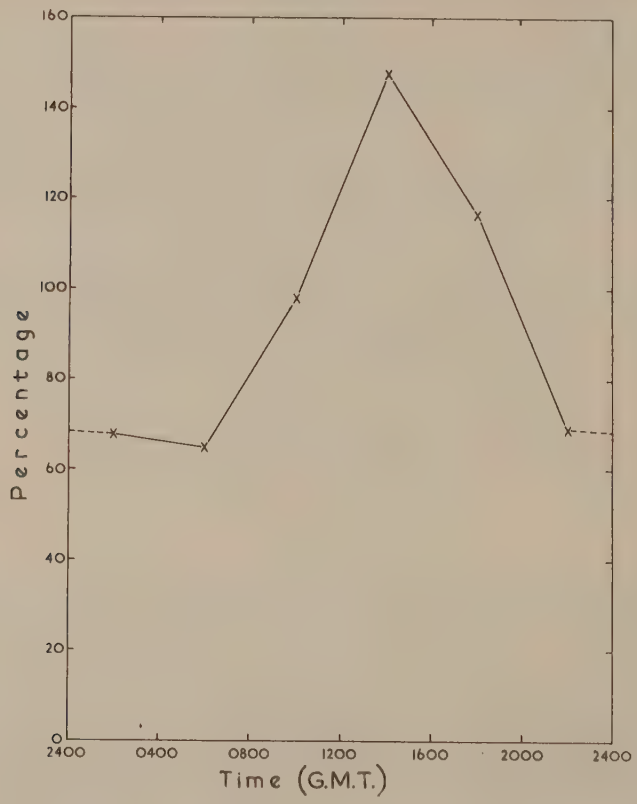

Figure 1. The diurnal change in numbers. Each point represents the percentage of the average numbers caught per standard haul for the day, averaged for each four-hour period.

(b) The diurnal variation in length

The length distributions were grouped into the same four-hour periods, as above, and means were taken of the total distributions. The four-hourly mean lengths are plotted in Figure 2, which shows that the smallest fish predominate between 1200 hours and 2000 hours. Larger fish were found between 2000 hours and 1000 hours, (this evidence is based on the samples from "Anton Dohrn" only); hence this value may be biased, being from only two positions. If the true diurnal variation in length were related to light intensity, it would be reasonable to expect that it would be centred about midday; the change, however, is so sharp as to suggest that a change of position might be responsible. Table 1 shows that this is not so. In fact, inspection of Table 3 shows that the smallest fish are caught at about midday *on each day*.

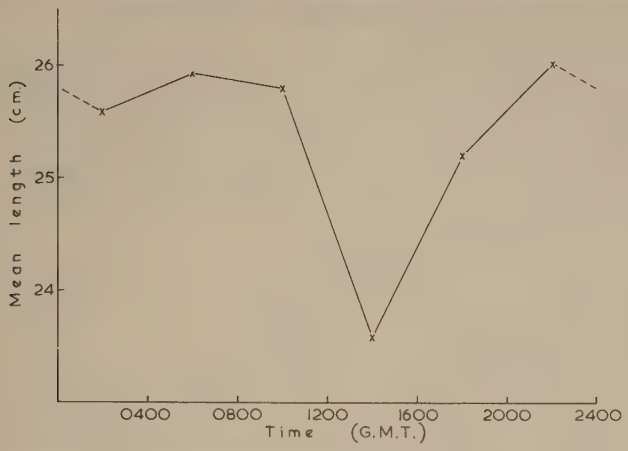

Figure 2. The mean length of fish caught in each four-hour period.

(c) The diurnal variation in the proportions of different maturity stages

In each haul for which the information is available, the fish were separated into immature, full, and spent. The numbers caught per hour's haul in each of the three categories were averaged for each four-hour period. Figure 3 shows the results, which are plotted from the data given in Table 2. The numbers/hr are grouped in four-hour periods as immature, spent, and full. Slight adjustments were made to these totals for the hauls made at intermediate times and for hauls lasting only half an hour. The smallest number of spent fish is found between 0800 hours and 1600 hours and the largest number of full fish and immature fish between 1200 hours and 1600 hours. The separation between spent fish, and full and immature (see Table 2), is greatest between 1200 hours and 1600 hours, which is the same period during which the peak in numbers was found.

Discussion

The three figures show a diurnal variation in numbers, in length, and in the proportion of the three stages of maturity. All trawl hauls were averaged for each day and each haul was expressed as a percentage of that average (Table 2 gives the percentages for the data given in Figure 3); the percentages were grouped in four-hour periods and averaged. Hence the measure of diurnal variation is independent of position changes from day to day; Table 3 shows that the change of position on one day was not great. Similarly it is unlikely that the diurnal variations in length and maturity stages are biased by changes in position.

The greatest proportion of full and immature herring was caught about midday or a little after. It is also true that the smallest fish were caught then.

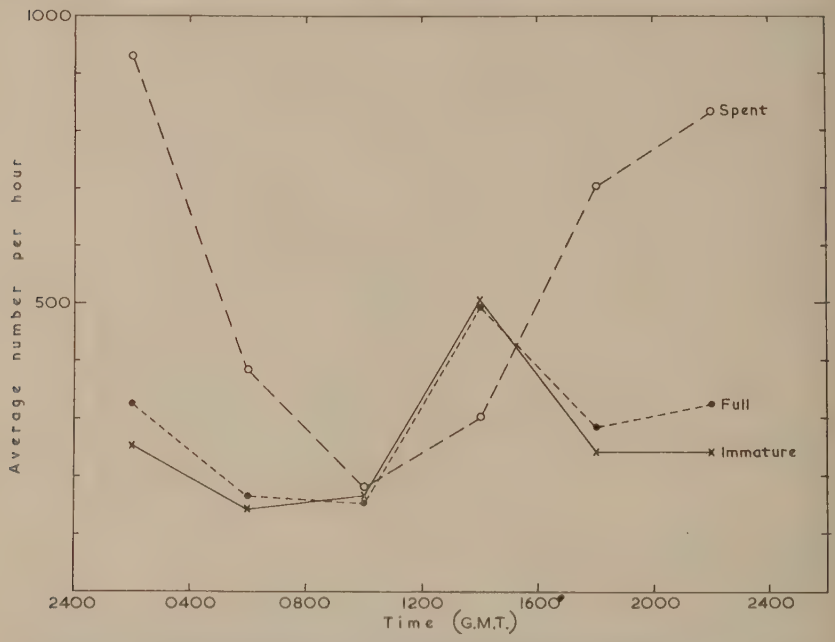

Figure 3. The diurnal variation in the average number of fish caught per hour's haul as full, immature, and spent at different times of the day and night.

Table 2

Average numbers of herring caught per hour in each maturity group, and percentage of the total number per hour, in 4-hour periods

4-hour period	No. of hauls	Immature		Spent		Full	
		No./hr	%	No./hr	%	No./hr	%
2400–0359	3	253	16·7	933	61·7	327	21·6
0400–0759	15	143	20·5	386	55·5	167	24·0
0800–1159	18	165	33·3	180	36·2	151	30·5
1200–1559	11	505	38·7	306	23·4	496	37·9
1600–1959	9	242	19·7	706	57·3	284	23·0
2000–2359	4	244	17·3	835	59·3	329	23·4

Thus it appears likely that the mean length of the total catch is reduced at that period by the immature fish coming to the bottom and by spent fish leaving it. This would suggest, firstly, that spent and full fish of the same length have opposed behaviour, the full fish sinking to the bottom at midday and spent fish rising from it; and, secondly, that the smaller immature fish behave as fulls. An interesting point is the sharp difference between the fulls and spents — with the spents leaving the bottom at midday and the fulls sinking to it then. Thus the act of spawning, the change from full to spent, must lead to a decrease in light sensitivity; perhaps spawning takes place at midday.

Summary

A diurnal variation in the numbers of trawl-caught herring was shown, the greatest quantity being caught at or near midday. The mean length was least in the afternoon and greatest at night. Immature and full fish were caught in greatest numbers at or near midday and the least numbers of spent fish were caught at this time; this difference accounts for the diurnal variation in mean length. It was thought possible that spent fish were found in higher light intensities than were immature or filling fish.

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Table 3

Mean lengths and numbers/hr of herring caught at each position

Cruise	Station	Position		Date	Time		Catch	
					Shot	Haul	Number per hour	Mean length (cm)
"Sir Lancelot" XIII, 1956	14	55°20′N	00°10′E	25. Aug.	0625	0730	31	28·47
	15	55°20′	00°09′		0806	0911	147	26·67
	16	55°19′	00°21′		0950	1051	888	27·87
	17	55°15′	00°08′		1130	1230	1274	27·42
	19	55°17′	00°10′		1740	1930	987	27·63
	20	55°20′	00°07′	26. Aug.	0455	0555	156	26·61
	21	55°16′	00°02′W		0655	0755	284	27·06
	22	55°15′	00°02′E		0830	0930	150	25·51
	23	55°18′	00°09′		1100	1200	700	26·59
	24	55°19′	00°00′		1236	1345	350	26·30
	25	55°21′	00°09′		1410	1510	700	27·28
	26	55°24′	00°04′		1555	1655	1400	27·15
	27	55°25′	00°00′		1742	1850	190	27·90
	33	55°00′	00°56′W	28. Aug.	0920	1031	1000	24·62
	34	54°57′	00°56′		1154	1307	265	23·47
	35	55°01′	00°57′		1600	1710	720	21·96
	36	55°02′	00°55′		1810	1900	472	22·78
"Sir Lancelot" XIV, 1956	34	54°48′N	01°14′E	8. Sept.	0525	0655	72	26·72
	35	54°50′	01°16′		0745	0845	54	26·80
	36	54°45′	01°12′		0950	1150	48	27·77
	37	54°42′	01°00′		1226	1400	14	27·95
	38	54°45′	01°09′		1540	1640	Nil	–
	44	55°22′	01°08′W	11. Sept.	0520	0630	500	25·61
	45	55°24′	01°04′		0740	0900	280	26·28
	46	55°28½′	01°01′		0945	1100	450	26·01
	47	55°23′	01°04′		1205	1305	410	25·70
	48	55°22′	01°04½′		1355	1525	235	25·84
	49	55°25½′	01°04′		1750	1850	810	25·68
	50	55°20½′	01°00′	12. Sept.	0530	0700	232	24·58
	51	55°18½′	01°04½′		0740	0910	500	24·16
	52	55°22′	01°07′		1010	1145	700	24·06
	53	55°20′	01°01′		1235	1335	1000	23·76
	54	55°22′	01°05′		1430	1545	1200	23·85
	55	55°26′	01°05½′		1703	1750	4700	24·23
	56	55°26′	01°12′	13. Sept.	0550	0730	480	26·88
	58	55°22′	01°00′		1045	1230	186	23·51
	59	55°18′	00°57′		1330	1450	600	23·34
	60	55°22′	01°03′		1545	1715	700	23·18
	61	55°25′	01°07′		1750	1850	2	–
"Sir Lancelot" XV, 1956	5	53°57′N	02°15′E	22. Sept.	0530	0555	220	26·07
	6	53°56′	02°14′		0640	0740	180	26·92
	7	53°57′	02°13′		0830	0930	33	26·23
	8	53°58′	02°11′		1020	1120	49	25·87
	9	54°00′	02°09′		1250	1405	1400	25·97
	10	54°02′	02°12′		1450	1550	1428	25·55
	11	54°00′	02°05′		1650	1750	111	26·13
	12	54°03′	02°05′	23. Sept.	0530	0630	375	26·17
	13	53°56′	02°12′		0805	0905	1000	26·30
	14	54°00′	02°13½′		0950	1050	850	26·82
	16	54°02′	02°09′	24. Sept.	0550	0650	10	24·80
	17	54°00′	02°17′		0730	0830	28	24·71
	18	54°03′	02°15′		0950	1050	120	25·81

Cruise	Station	Position		Date	Time		Catch	
					Shot	Haul	Number per hour	Mean length (cm)
"Sir Lancelot" XVI, 1956	1	54°13′N	02°23′E	8. Oct.	0640	0750	46	27·60
	2	54°11′	02°19½′		0930	1005	663	26·75
	3	54°10′	02°14′		1040	1140	1	–
	4	54°08′	02°13′		1212	1322	10	–
	5	54°02′	01°49′		1630	1735	14	–
	6	54°17′	01°53′	9. Oct.	1115	1300	4	–
	7	54°27′	01°28′		1453	1610	17	–
	8	54°28′	01°22′		1637	1730	227	23·73
	9	54°25′	01°20′	10. Oct.	0545	0705	175	24·33
	10	54°23′	01°22′		0735	0835	1638	22·25
	11	54°17′	01°24′		0916	1030	125	22·64
	12	54°20′	01°22′		1100	1230	486	22·63
	13	54°16′	01°16′		1300	1430	100	23·81
	14	54°13′	01°11′		1515	1615	75	–
	17	54°18′	01°17′	11. Oct.	0540	0710	42	27·13
	18	54°13′	01°14′		0745	0915	88	23·22
	19	54°08′	01°25′		0950	1120	27	23·88
	20	54°03′	01°31′		1350	1520	284	28·92
"Anton Dohrn"							Number per ½ hour	
1957	2020A	57°27′N	01°57′E	25. Sept.	2010	2040	101	28·41
	B				2230	2300	213	28·43
	C			26. Sept.	0230	0300	221	27·66
	D				0535	0605	84	27·83
	E				0725	0755	223	28·28
	F				0930	1000	66	28·67
	G				1235	1305	1300	29·37
	H				1640	1710	475	27·69
	I				1745	1815	254	26·95
	J				2030	2100	51	26·81
	2021	56°00′	02°00′	27. Sept.	1100	1130	1400	27·55
	2022	55°30′	01°56′		1540	1610	173	27·39
	2024	55°16′	01°48′		1805	1835	113	30·14
	2064A	55°10′	00°20′	1. Oct.	1725	1755	453	25·48
	B				1940	2010	2826	25·70
	C				2100	2130	2454	25·71
	D				2400	2430	1980	25·36
	E			2. Oct.	0245	0315	71	25·61
	F				0535	0605	2288	25·58
	G				0700	0730	776	25·57
	H				0950	1020	1215	24·73
	I				1305	1335	3630	19·01
	J				1710	1740	197	18·24

Table 4

Percentage length distribution of herring caught at each station

A. "Sir Lancelot", Cruise XIII, 1956

Length (cm)	Station number 12	14	15	16	17	19	20	21	22	23	24	25	26	27	30*	31*	33	34	35	36
17	–	–	–	–	–	–	–	–	–	–	–	–		–		–		0·9	–	–
18	–	–	–	–	–	–	–	–	–	–	–		–	–	–	0·5	0·5	2·5	4·3	2·5
19	–	–	–	–	–	0·3	–	–	0·7	0·6	–		0·4		0·6	–	1·6	3·4	5·7	8·2
20	–	–	–	–	–	–	–	–	–	–		–	–	–	1·5	2·2	1·8	6·8	16·7	19·5
21	–	–	–	–	–	0·3	–	–	–	0·6	–	0·9	0·4	–	10·2	8·6	6·2	9·6	25·3	31·7
22	–	–	2·5	0·3	0·3	0·6	0·6	–	8·0	–	–	0·9	0·4	–	27·5	26·9	10·9	15·2	26·0	20·5
23	1·2	–	4·4	1·1	2·5	0·8	7·1	2·1	10·7	6·9	9·8	1·8	2·3	0·9	36·2	30·1	17·9	21·7	12·8	9·2
24	1·2	2·9	12·6	5·2	4·1	5·2	7·1	6·9	22·7	14·5	17·2	4·4	6·5	3·3	15·0	18·3	17·9	19·2	5·3	4·3
25	4·8	2·9	15·1	7·7	10·7	8·8	18·6	20·0	20·7	18·2	19·7	15·0	15·7	8·8	5·1	5·9	13·5	8·7	1·8	1·7
26	17·8	5·9	24·5	18·6	23·6	19·0	30·1	22·8	16·0	15·1	23·0	20·9	22·1	16·7	2·7	4·3	17·9	5·9	1·1	1·0
27	36·9	32·4	20·1	19·8	23·6	25·1	20·5	21·4	12·7	19·5	12·3	23·5	22·1	27·0	1·2	1·1	8·8	2·8	0·7	0·7
28	21·4	20·6	9·4	19·2	17·6	17·1	7·7	11·0	4·7	14·5	8·2	15·0	16·0	17·2	–	2·1	1·6	2·8	0·3	0·7
29	9·5	11·8	5·7	15·2	10·4	11·9	3·2	11·7	2·6	5·0	4·9	10·0	6·1	11·6	–	–	1·3	0·6	–	–
30	3·6	20·6	3·8	8·9	6·3	8·6	3·8	3·4	0·6	4·4	4·9	6·8	6·1	10·7	–	–	–		–	–
31	3·6	2·9	1·9	3·4	0·8	2·2	1·3	0·7	0·6	0·6	–	0·9	1·9	3·3	–	–	–	–	–	–
32	–	–	–	0·6	–	–	–	–	–	–	–	–	–	0·5	–	–	–	–	–	–

B. "Sir Lancelot", Cruise XIV, 1956

Length (cm)	Station number 34	35	36	37	44	45	46	47	48	49	50	51	52	53	54	55	56	58	59	60
16	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–		0·6	–	–
17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0·3	–	–	2·5	0·7	0·2
18	–	–	2·1	–	–	–	–	0·4	–	–	–	0·3	0·8	–	0·8	0·2	–	1·8	1·5	2·9
19	–	–	1·0	–	–	–	–	–	0·3	0·3	–		0·8	0·5	2·4	–	–	3·4	1·0	3·3
20	–	–	–	–	–	1·0	–	0·4	0·3	–	1	1·1	1·3	2·8	4·3	0·5	–	1·5	4·7	4·8
21	0·9	–	–	–	0·5	1·0	0·8	1·4	0·6	1·2	3	6·2	8·0	6·7	8·3	3·9	–	4·3	11·0	11·7
22	2·8	3·7	2·1	–	11·3	3·6	7·6	6·0	6·2	7·4	20	19·6	20·2	26·9	17·1	17·3	0·8	20·3	24·2	24·6
23	13·0	7·4	1·0	4·5	19·1	8·3	10·9	13·4	13·2	14·2	19	23·9	21·0	26·1	23·8	30·2	5·1	25·5	27·0	25·4
24	11·1	9·3	5·2	4·6	12·1	11·3	14·1	15·5	13·0	17·3	20	24·2	20·5	16·3	18·4	21·4	11·6	19·7	11·7	11·7
25	7·4	22·2	6·3	4·5	12·3	16·0	16·2	15·9	20·8	17·3	11	9·2	10·6	9·6	7·0	10·9	13·5	9·2	10·5	6·7
26	16·7	13·0	10·4	13·6	16·1	20·0	19·9	20·8	20·0	17·6	15	7·6	9·6	6·2	10·2	9·5	19·5	7·4	4·3	3·6
27	20·4	16·7	19·8	31·8	14·1	19·3	13·4	15·2	11·0	10·5	6	4·1	4·5	2·1	4·5	3·9	22·2	2·2	2·5	2·9
28	8·3	7·4	19·8	9·1	8·5	13·3	7·3	6·4	7·3	6·8	4	2·4	1·6	2·3	2·1	1·0	16·2	1·5	0·7	1·4
29	10·2	11·1	16·7	9·1	3·5	4·3	6·3	3·2	4·8	4·0	1	0·8	0·8	0·5	0·8	1·0	7·0	–	0·2	0·2
30	7·4	3·7	11·5	18·2	1·8	1·3	2·8	1·4	1·4	3·1	–	0·3	0·3	–		–	3·2	–	–	0·5
31	1·8	5·6	2·1	4·6	0·7	0·6	0·7	–	0·6	0·3		0·3	–	–	–	–	0·5	–	–	–
32	–	–	1·0	–	–	–	–	–	0·6	–	–	–	–	–	–	0·2	0·3	–	–	–
33	–	–	1·0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

(* Larsson midwater trawl).

Table 4 (continued)

C. "Sir Lancelot", Cruise XV, 1956

Length (cm)	Station number 1	2	5	6	7	8	9	10	11	12	13	14	18
17	–	0·5	–	–	–	–	–	–	–	–	–	–	–
18	–	0·3	–	–	–	–	–	–	–	0·3	–	–	1
19	–	2·3	–	–	–	–	–	–	–	–	0·8	–	3
20	–	3·8	–	–	–	–	–	–	–	–	–	–	3
21	–	5·1	–	–	–	–	–	0·5	–	0·3	0·3	1	2
22	4	10·7	–	3	–	4	1·8	4·2	–	0·5	1·6	–	1
23	4	28·5	15	–	9	10	11·3	12·0	9·9	8·3	5·7	7	14
24	14	21·9	22	12	15	18	17·3	25·2	24·3	18·4	12·8	6	29
25	8	14·2	11	11	15	16	15·4	15·9	14·4	17·6	21·3	15	19
26	34	6·6	22	27	27	25	27·5	23·0	20·7	21·6	25·1	22	19
27	14	5·1	13	23	21	18	17·8	13·5	17·1	20·3	20·4	26	7
28	14	1·0	13	14	12	6	7·3	4·2	7·2	8·8	6·3	14	2
29	4	–	–	6	–	2	0·8	1·0	3·6	2·4	3·8	5	–
30	2	–	4	1	–	–	0·8	0·5	–	1·6	2·4	4	–
31	2	–	–	3	–	–	–	–	2·7	–	–	–	–

D. "Sir Lancelot", Cruise XVI, 1956

Length (cm)	Station number 1	2	8	9	10	11	12	13	17	18	19	20
16	–	–	–	–	0·2	–	–	–	–	–	–	–
17	–	–	0·7	–	0·5	1·1	–	–	–	1·0	–	0·3
18	–	–	1·4	1·7	3·7	2·3	4·5	2·4	–	1·0	–	0·3
19	–	–	1·4	2·2	7·0	17·0	7·8	3·9	–	9·7	2·5	0·5
20	–	–	6·3	6·1	11·5	12·5	12·1	7·1	–	8·7	–	2·0
21	–	–	8·5	3·0	20·5	11·4	13·0	11·8	–	8·7	7·5	3·7
22	6	0·4	21·8	13·5	24·0	18·2	20·0	7·1	1·7	11·7	17·5	26·2
23	8	9·1	23·2	16·5	20·1	13·6	17·3	19·7	1·7	25·2	42·5	33·9
24	10	17·1	12·7	15·2	5·5	6·8	14·0	21·3	15·2	12·6	7·5	12·0
25	2	14·3	9·9	18·3	2·9	3·4	4·3	11·0	6·8	9·7	7·5	5·2
26	6	13·9	4·9	13·5	2·6	3·4	3·9	6·3	13·6	3·9	5·0	6·0
27	20	17·4	1·4	7·4	0·9	2·3	1·4	3·9	30·5	5·8	7·5	5·7
28	8	10·4	3·5	1·3	0·4	3·4	1·2	1·6	16·9	1·9	2·5	3·0
29	20	9·1	2·8	–	0·2	3·4	0·4	3·1	8·5	–	–	0·5
30	18	5·9	1·4	0·9	–	1·1	–	0·8	3·4	–	–	0·7
31	–	2·1	–	0·4	–	–	–	–	1·7	–	–	–
32	2	0·3	–	–	–	–	–	–	–	–	–	–

Table 4 (continued)

E. "Anton Dohrn", Cruise 1957

Length (cm)	Station number																			
	2019	2020A	2020B	2020C	2020D	2020E	2020F	2020G	2020H	2020I	2020J	2064A	2064B	2064C	2064D	2064E	2064F	2064G	2064H	2064I	2064J
8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0·5
9	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	1·0
10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0·5	–	2·7	4·6
11	–	–	–	–	–	–	–	–	–	0·4	–	0·3	–	–	–	–	–	0·2	–	11·2	10·7
12	–	–	–	–	–	–	–	–	–	–	–	1·3	–	–	–	–	0·7	0·8	0·7	24·1	25·4
13	–	–	–	–	–	–	–	–	–	–	–	2·3	–	–	–	–	–	0·5	0·5	10·5	12·2
14	–	–	–	–	–	–	–	–	–	–	–	0·3	–	–	0·2	–	–	1·3	0·7	1·8	1·0
15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0·3	–	–	–	–
16	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0·2	–	–	–	–	–	–
20	–	–	–	–	–	–	–	–	–	–	–	0·2	–	–	–	–	–	–	0·3	–	–
21	0·5	–	–	–	–	–	–	–	–	–	–	–	–	–	0·2	1·4	0·3	–	3·5	0·1	0·5
22	–	–	–	–	–	–	–	–	–	1·2	2·0	3·0	2·7	1·0	2·5	1·4	2·6	2·1	8·9	1·4	1·0
23	2·4	3	0·7	3·2	–	2·2	–	–	2·9	4·7	3·9	19·3	17·0	13·4	15·7	12·7	15·4	19·1	23·7	9·2	9·1
24	11·8	9	4·2	6·8	9·5	2·7	3·0	2·7	11·8	12·2	23·5	16·5	22·9	27·9	33·2	36·6	25·2	9·8	19·0	11·4	11·7
25	16·0	10	13·3	17·2	21·4	15·7	16·7	6·2	16·8	19·3	13·7	10·4	18·6	18·8	16·6	14·1	15·9	22·4	16·3	8·9	7·1
26	18·4	10	18·9	21·7	11·9	13·9	7·6	6·7	13·7	16·5	15·7	10·7	11·8	15·9	13·4	11·3	12·7	12·9	8·6	4·5	2·5
27	14·6	7	6·3	6·3	9·5	9·4	7·6	4·0	7·6	12·6	3·9	15·2	12·4	10·3	8·4	7·0	13·2	10·6	10·6	6·4	5·1
28	10·4	12	8·4	11·3	10·7	11·2	13·6	13·3	13·1	13·4	13·7	12·9	10·5	8·6	6·6	8·5	10·3	12·1	4·7	6·1	5·1
29	10·9	15	15·4	14·0	13·1	15·7	19·7	22·2	12·4	9·4	15·7	5·3	3·8	4·1	2·3	2·8	2·4	6·4	1·7	1·7	1·5
30	10·8	23	20·3	13·1	16·7	18·4	18·2	25·8	13·1	6·7	5·9	1·5	0·3	–	0·5	4·2	1·0	1·0	0·3	–	1·0
31	3·3	9	10·4	5·4	6·0	10·8	9·1	16·4	7·6	2·4	2·0	0·8	–	–	–	–	–	0·3	0·5	–	–
32	0·9	1	0·7	0·5	1·2	–	4·5	2·7	0·6	1·2	–	–	–	–	0·2	–	–	–	–	–	–
33	–	1	1·4	0·5	–	–	–	–	0·4	–	–	–	–	–	–	–	–	–	–	–	–

Table 5

Mean lengths of immature, spent, and full herring at various stations

Cruise	Date		Time of	Numbers of fish per standard haul*) and mean length (cm)							
				Immature		Spent		Full		Total	
"Sir Lancelot"		Station	shot	No.	$\bar{x}$	No.	$\bar{x}$	No.	$\bar{x}$	No.	$\bar{x}$
XIII, 1956	25. Aug.	14	0625	1	27·50	–	–	30	28·50	31	28·47
		16	0950	193	26·98	540	28·32	155	27·39	888	27·87
		19	1740	189	27·26	448	27·90	350	27·48	987	27·63
	26. Aug.	20	0455	41	26·01	64	26·91	51	26·72	156	26·61
		21	0655	57	26·22	140	27·52	87	26·87	284	27·06
		22	0830	64	25·06	31	26·31	55	25·59	150	25·51
		23	1100	226	26·00	164	26·30	310	27·14	700	26·59
		25	1410	76	26·12	89	27·37	535	27·44	700	27·28
		26	1555	403	26·47	399	28·24	598	26·90	1400	27·15
		27	1742	27	28·57	57	27·73	106	27·80	190	27·90
XIV, 1956	8. Sept.	34	0525	9	23·88	1	26·50	62	27·12	72	26·72
		35	0745	5	24·10	–	–	49	27·07	54	26·80
		36	0950	3	21·10	1	27·00	44	28·16	48	27·77
		37	1226	1	23·50	–	–	13	28·17	14	27·95
	11. Sept.	44	0520	215	24·46	33	27·59	264	26·31	512	25·61
		46	0945	159	24·71	123	26·87	193	26·53	475	26·01
		47	1205	153	24·46	84	26·37	188	26·35	425	25·70
		48	1355	85	25·01	43	26·41	109	26·17	237	25·84
	12. Sept.	50	0530	121	23·63	58	25·59	53	25·65	232	24·58
		51	0740	278	23·53	204	24·93	7	26·50	490	24·16
		53	1235	908	22·95	408	24·41	554	24·62	1870	23·76
XV, 1956	22. Sept.	6	0640	–	–	–	–	180	26·92	180	26·92
		7	0830	1	23·50	–	–	32	26·31	33	26·23
		8	1020	1	22·50	–	–	48	25·94	49	25·87
		9	1250	32	23·69	–	–	1368	26·02	1400	25·97
		10	1450	132	25·20	42	26·17	1254	25·57	1428	25·55
		11	1650	6	24·67	3	26·50	102	26·21	111	26·13
	23. Sept.	12	0530	56	25·70	39	26·29	280	26·24	375	26·17
		13	0805	22	23·73	146	26·45	199	26·48	367	26·30
		14	0950	8	26·50	290	27·31	552	26·57	850	26·82
XVI, 1956	10. Oct.	9	0545	52	21·77	83	25·38	40	25·42	175	24·33
		10	0735	1247	21·65	121	25·19	270	23·72	1638	22·25
		11	0916	79	20·98	7	25·36	39	25·58	125	22·64
		12	1100	324	21·55	82	25·17	80	24·38	486	22·63
		13	1300	29	20·91	5	25·50	66	25·00	100	23·81
	11. Oct.	17	0540	3	24·83	4	26·00	35	27·36	42	27·43
		18	0745	52	21·96	26	24·92	10	24·70	88	23·22
		19	0950	5	21·70	2	26·50	20	24·15	27	23·88
		20	1350	71	22·50	49	25·68	164	23·98	284	23·92
"Anton Dohrn" 1957	25. Sept.	2020A	2010	11	27·13	45	27·88	44	29·14	101	28·41
		B	2230	17	27·53	116	27·80	78	29·69	213	28·43
	26. Sept.	C	0230	48	26·92	85	27·05	86	28·56	221	27·66
		D	0535	25	27·10	33	27·32	26	29·19	84	27·83
		E	0725	12	25·92	92	28·35	119	28·47	223	28·28
		F	0930	5	27·50	44	28·50	17	29·44	66	28·67
		G	1235	7	26·21	130	28·89	188	29·81	325	29·37
		H	1640	66	25·61	217	27·47	187	28·53	475	27·69
		I	1745	33	25·32	157	27·25	61	27·29	254	26·95
		J	2030	34	26·71	2	27·00	15	27·03	51	26·81
	1. Oct.	2064A	1725	89	22·56	266	26·23	98	26·10	453	25·48
		B	1940	470	24·08	2027	26·22	329	24·78	2826	25·70
		C	2100	425	25·43	1507	25·88	522	25·45	2454	25·71
		D	2400	326	24·10	1262	25·85	392	24·86	1980	25·36
	2. Oct.	E	0245	5	24·70	53	25·63	13	25·88	71	25·61
		F	0535	75	20·71	1965	25·73	248	25·89	2288	25·58
		G	0700	58	19·03	533	26·19	183	25·76	776	25·57
		H	0950	147	21·74	758	25·45	310	24·40	1215	24·73
		I	1305	2026	13·63	1192	25·68	412	26·16	3630	19·01
		J	1710	119	13·26	55	25·90	23	25·67	197	18·24

* Standard haul is 1 hour for "Sir Lancelot" cruises and ½ hour for "Anton Dohrn".

Utilization of Food by a Bermuda Reef Fish, *Epinephelus guttatus**

By

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Introduction

The most common approach to the study of fish nutrition has established the relation between the weight of food eaten and weight gain. Workers (DAWES, 1930–31; MOORE, 1941; SCHOLZ, 1932; PENTELOW, 1939; and others) obtained highly conflicting results. Diversity however, was to be expected since weight gain is dependent on several variables, such as the nutritional value of food, differential rates of fat and protein deposition, etc. Results of the foregoing workers pointed to the need for considerable refinement in the methods of study of food utilization by fishes. The first such attempts were made by investigators at the Cortland Fish Hatchery in determining the biological value of different proteins, and the dietary requirements of trout (MCCAY *et al.*, 1927, 1931; TUNISON, 1940; TUNISON and MCCAY, 1935). Later, IVLEV (1939) considered the problem from the aspect of energy transfer in carp. Most recently, GERKING (1952, 1954, 1955) has investigated protein utilization by centrarchids. Notably lacking is information on the utilization of food by marine teleosts, or an attempt to incorporate all of these approaches.

This study was initiated to measure the relative efficiency with which the red hind (*Epinephelus guttatus*) utilizes its food for growth and maintenance and to assay the effect of seasonal temperature fluctuations and size of fish on food utilization.

Methods

The red hind is the most abundant serranid of the Bermuda reefs. It is found at all depths down to at least 80 m, and attains a length of about 45 cm and a weight of 1,400 g.

Stomach samples, taken at different times of the year, revealed little variation

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in the food habits of fish of different sizes (130 to 1,200 g), and no appreciable change in diet from season to season. The most common organisms in stomachs were various crustacea, although fish were also eaten. Crabs of the genus *Callapa* and shrimp of the family Alphiidae were the most abundant crustaceans. The fishes fed upon consisted almost entirely of species of the family Labridae, with *Thalassoma bifasciatum* (Bloch) making up the largest proportion.

Three feeding experiments of 21 days each were conducted at average water temperatures of 19°, 23°, and 28°C (±1°C). Three experimental groups of fish were composed of from 8 to 12 individuals that were fed together. Group 1 included fish from 135 to 245 g, Group 2 fish weighed 245 to 450 g, and Group 3 fish weighed 510 to 710 g.

Each group was fed a surplus of food once a day, and unused material was removed from the tanks after one hour. Different species of fish were used for food during each of the feeding periods. These included *Anchoa choerostoma*, *Sardinella anchovia*, and *Harengula callolepis* which were used at 19°, 23°, and 28°C respectively.

Faeces were removed from the tanks daily with a siphon tube. The included water was passed through No. 2 plankton netting, collected and refiltered through a Buchner funnel with a No. 1 Whatman filter paper.

Changes in the body composition of experimental fish were determined by the "sacrifice method" of MAYNARD and LOOSLI (1956). This method has the limitation that a number of individuals must be treated as a unit not only in their feeding but in the consequent determination of food utilization and the treatment of results. While thus masking individual variation within a group it nevertheless provides the only workable method for studying changes in the composition of living organisms.

Entire animals were homogenized, and then dried at 80°C for the determination of their chemical composition. The following methods were used in the analysis of food, fish, and faeces:—

(1) Total nitrogen and non-protein nitrogen by the macro-Kjeldahl method (WILLARD and FURNHAM, 1940). Non-protein nitrogen was extracted with trichloracetic acid and the value obtained subtracted from the total nitrogen to give the amount of protein nitrogen present.

(2) Fat, according to the Association of Official Agricultural Chemists (1950).

(3) Caloric content by combustion of one-half gramme samples in an oxygen bomb calorimeter (Parr Instrument Co., 1948).

Results and Discussion

1. Absorption of foods

Red hinds absorbed between 89 and 98% of the fats and proteins from their food (Table 1). Other investigators have found equally high values for absorption. TUNISON and MCCAY (1935) showed that brook trout, maintained at 8°C, removed between 80 and 90% of the fats from their food. GERKING (1952, 1954) found that between 95.7 and 98.4% of the protein in food was absorbed by three species of centrarchids. Approximately 89% of the energy contained in the food of yearling carp was utilized by them (IVLEV, 1939).

The percentage of food absorbed did not vary with temperature or among different sizes of fish. Similar results concerning the relation between size and

Table 1

Effectiveness with which food was absorbed from the intestine by experimentally fed red hinds $\left(\frac{\text{intake} - \text{excrement}}{\text{intake}} \times 100\right)$

	Protein			Fat			Energy		
	19°C	23°C	28°C	19°C	23°C	28°C	19°C	23°C	28°C
Group 1	96·3	–	96·7	95·1	–	89·3	96·2	–	97·3
Group 2	97·2	92·2	97·5	96·1	92·7	88·7	96·4	91·3	96·8
Group 3	95·7	89·0	97·6	94·7	96·3	92·3	95·7	92·2	96·5

Table 2

Efficiencies with which red hinds utilized various portions of their diet for growth

	°C	Weight coefficient	Protein efficiency	Fat efficiency	Energy coefficient
Group 1	19	21·9	29·4	50·5	36·8
	23	–	–	–	–
	28	24·7	32·1	153·6	42·5
Group 2	19	17·6	22·4	43·3	30·3
	23	16·0	24·1	52·8	34·8
	28	15·3	22·7	158·3	35·5
Group 3	19	16·1	18·8	18·8	18·3
	23	18·7	22·7	10·3	16·5
	28	17·7	20·6	61·0	24·3

protein absorption (GERKING, 1952) and fat absorption (TUNISON and MCCAY, 1935) have been reported. ARNOLDI and FORTUNATOVA (1937) reported that *Gobius cephalarges* absorbed between 88 and 89% of its food at 19°C, but that there was a marked decrease at lower temperatures (75% at 10°C). Similar results with carp were obtained by KARZINKIN (1935). The lower temperature in each case was considerably below minimum water temperatures at Bermuda and may explain the difference in results.

2. Weight increase and feeding rates

Weight coefficients, defined as $\frac{\text{weight gain}}{\text{weight of food}} \times 100$ have frequently been used to express the efficiency with which food is utilized for growth. Values obtained for the red hind suggested little difference in conversion coefficients between fish of Groups 2 and 3, but values for Group 1 fish were somewhat higher (Table 2). RICKER (1946) has pointed out that small fish of a species gain more weight than large ones per unit weight of food intake. This may not be a strict function of size although large differences between the fish probably demonstrate the postulated relation. Fish of Groups 2 and 3 obviously made equally efficient use of the food; their weight coefficient ranged between 15·3 and 18·7%. In addition, temperature did not influence weight coefficients. A relative increase of 2·6 times in food consumption, per unit body weight, in Group 1 fish between 19° and 28°C yielded a 2·9 fold increase in weight. Group 2 fish at 28°C ate 2·3 times more than that eaten at 19°C and their

Table 3

Starting weight, relative weight gain, and feeding rates of experimentally fed red hinds*

	°C	Number of fish	Starting weight in g	Weight gain in 21 days (% of body weight)	Feeding rate/day (% of body weight)
Group 1	19	6	260–335	5·5–16·3	
			(269)	(12·2)	(2·6)
	28	8	133–248	25·5–43·4	
			(184)	(35·2)	(6·8)
Group 2	19	10	355–468	2·6–9·7	
			(411)	(6·4)	(1·7)
	23	8	257–433	2·9–10·6	
			(309)	(6·2)	(1·8)
	28	6	335–474	9·7–14·9	
			(368)	(12·8)	(4·0)
Group 3	19	12	533–732	2·7–8·7	
			(610)	(5·9)	(1·7)
	23	6	503–763	1·8–10·3	
			(625)	(7·7)	(2·0)
	28	6	507–637	8·6–25·1	
			(600)	(15·7)	(4·2)

* The ranges are given with means in parentheses.

weight increased twice. When Group 3 fish increased their intake 2·5 times their weight increased 2·7 times (19° and 28°C). Among Group 2 and 3 fish there was no difference in the rate of feeding or weight gain at 19° and 23° (Table 3).

3. Protein efficiency

Protein efficiency has been defined as $\frac{\text{amount of protein synthesized}}{\text{amount of protein absorbed}} \times 100$ (MAYNARD and LOOSLI, 1956). Efficiencies measured over 21 day periods were higher among small fish (Group 1) than among large ones (Groups 2 and 3). Comparison with data from bluegills indicates that this relationship is probably not best expressed as a simple regression as GERKING (1955) postulated. Rather it appears that efficiency was high among small fish, that it fell rapidly with increase in size, and gradually levelled off at about 20% (Table 2). Whether this final change occurred at the age of approaching sexual maturity is not known although inspection of the gonads suggested that this was likely.

There was no apparent difference in the efficiency with which protein was utilized for growth at different temperatures. In fishes, both the rate of digestion (RIDDLE, 1909) and of metabolism (PROSSER, 1950) slow down with a fall in temperature. Therefore, it is likely that at any one temperature the fish fed at a rate that allowed for maximum digestion.

4. Utilization of fats

The efficiency with which fats are utilized is considerably more difficult to measure than protein efficiency. At 28°C, 53·6 and 58·3% more fat was deposited by Group 1 and 2 fish respectively than was ingested (Table 2). Considerable amounts of protein were, therefore, converted to fat, but since mixed diets were fed it was not possible to measure this change. It is possible that the

bulk of fat deposited was synthesized from protein sources if fat was used as a primary source of energy. PHILLIPS *et al.* (1957) have indicated that this may occur in brook trout.

5. Energy disposition

Energy derived from food may be egested, deposited in the form of protein or fat, or respired. IVLEV (1939) used the ratio $\frac{\text{calories deposited}}{\text{calories ingested}} \times 100 = K_1$ to express the relation between energy deposited in the body and energy intake.

Small red hinds (Group 1) utilized fats and proteins for growth with greater efficiency than did large fish (Groups 2 and 3). Whereas relatively more fat was deposited by Group 2 than by Group 3 fish, protein efficiency was nearly the same for both. Therefore, it may be shown that the smaller the fish the more energy was deposited per unit caloric intake (Table 2).

Previously, only IVLEV (1939) had determined energy coefficients for fish by calorimetric procedure. He showed that yearling carp had a K_1 of 31·3%. RICKER (1946) summarized the coefficients for fish obtained by a number of workers, and demonstrated an inverse relation between size and K_1. However, these calculations were based on weight coefficients and not on calorific procedures. When K_1 values are compared with weight coefficients (Table 2) it is obvious that one measurement may be entirely unrelated to the other. This is so because if one fish were to lay down nothing but protein and another nothing but fat, the one depositing protein would gain 8 times more weight, and yet deposit the same amount of energy (BRODY, 1945).

6. Relative growth

MAYNARD and LOOSLI (1956) have commented that true growth is "an increase in the structural tissues such as muscle and bone and also in the organs. It should be distinguished from the increase that results from fat deposition in the reserve tissues".

The relative increase in tissue components has been calculated in the following manner: $\frac{\text{Weight component deposited}}{\text{weight of component initially present in the body}} \times 100$. In the present experiments the relative rate of protein deposition was higher among small (Group 1) fish at any one temperature than among larger ones. Therefore, total relative growth (weight gain less fat) was significantly greater in this group (Table 4). This is explained by the faster feeding rates of small individuals, and the greater efficiency with which they utilized protein for growth. Total relative growth-rates on the other hand, were comparable among Group 2 and 3 fish in spite of the fact that more energy was deposited by Group 2 than by Group 3 fish.

It is apparent that temperature increase, between 23° and 28°C brought about a marked increase feeding rate (Table 3). A large difference in relative growth also existed. Therefore, since the percentage of food absorbed from the intestine and protein efficiency were not influenced by temperature the amount of tissue synthesis occurring was controlled directly by the amount of food eaten. This relation probably holds until food is ingested at a rate that does not permit efficient absorption. Such did not occur even when small fish (Group 1) were fed at a rate of 6·3% of their body weight per day.

Table 4

Relative increase of tissue constituents in the bodies of experimentally fed red hinds*

	Group 1		Group 2			Group 3		
	19°	28°	19°	23°	28°	19°	23°	28°
Protein	11·6	43·2	6·1	7·9	18·0	5·1	7·0	16·9
Water	10·2	30·4	5·8	4·2	9·9	5·6	8·5	15·1
Ash	7·8	19·9	3·1	5·8	3·4	8·8	0·1	14·1
Total relative growth**	10·4	32·2	5·7	5·1	11·0	5·7	7·7	15·4

* $\frac{\text{Weight of component deposited}}{\text{Weight of component initially present}} \times 100.$

** Weight gain due to fat has been eliminated.

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Summary

1. Three sizes of the red hind (*Epinephelus guttatus*) were fed in the laboratory at three different temperatures to determine the efficiency with which it utilizes food for growth.

2. Between 89% and 98% of the food ingested was absorbed from the intestine. There was no difference in the relative amount of protein and fat absorbed at different temperatures.

3. Relative weight gain and the amount of food eaten, increased markedly between 23° and 28°C, but not between 19° and 23°C. Small fish ate relatively more than large fish at any one temperature.

4. Protein efficiency was higher among small fish than large fish, and was not influenced by temperature.

5. The number of calories retained per unit caloric intake decreased with increase in the size of fish, and was not influenced by temperature.

6. The relative growth-rate of small fish was greater than that of large fish, and resulted from a combination of greater efficiency in the utilization of proteins and a higher rate of food intake.

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Letters to the Editor

Water Temperature and Cod Growth-Rate

HOLT's (1959) criticism of my paper "Cod growth and temperature" (TAYLOR, 1958a) necessarily draws attention to several misconceptions and misinterpretations of the von Bertalanffy (1938) growth function by BEVERTON and HOLT (1957) which these authors might have wished to emend in due course. These misconceptions result in rather serious errors in the interpretation both of the nature of growth and of the yield curves which result from variation in growth parameters.

BEVERTON and HOLT (1957, p. 105) regard variation of growth with density in fish populations as "perhaps the best established of the density dependent effects." They concede that while changes in food consumption may result in some change in general metabolic activity, "these changes are likely to be of minor importance compared with variations in the rate of anabolism that would result directly from considerable change in the rate of food consumption" (p. 106).

Their conclusion that the parameter E (H in HOLT's (1959) notation) is subject to environmentally-induced variation without concomitant variation in K is further confused by assuming that L_∞ (and thus W_∞) remains constant with a change in E. The result is their astonishing Figure 17·23 which shows four growth curves, representing four-fold changes in K, attaining the same asymptote. The substantial displacement of yield maxima on fishing intensity which should result from change in K does not, of course, appear in their Figure 17·22. With an assumed constancy in W_∞, it is easy to see from Figure 17·23 why HOLT considers that a change in K would result in no change in life-span, or average size composition of a population.

In a recent paper (TAYLOR, 1959) dealing with temperature and growth relations in the razor clam, *Siliqua patula*, I have shown that for many marine and freshwater species, the relation between E and K is a species-characteristic regression, both within and between environments. Recalling that $E = KL_\infty$, one can easily compute this regression for cod from the data of Table 1 (TAYLOR, 1958a, p. 367).

A characteristic regression between E and K, for every species we have examined for which the growth data are reasonably graduated by a von Bertalanffy equation, generalizes many aspects of fishery yield-assessment.

As for my alleged "misuse of terms" in defining "life-span", age and growth may be considered as irreversible processes and are defined by the von Ber-

talanffy function in terms of time and size. If HOLT is correct in stating that size at maturity in many fishes in 0·67 L_∞, then he may find it quite convenient to define, without ambiguity, the age at maturity of these fishes as

$$A_{0\cdot67} = 1\cdot109/K + t_0$$

For comparative purposes, and for estimating natural mortality limits, it is immaterial what fraction of time required to attain L_∞ we use. Perhaps for this purpose it would be more logical to use $A_{0\cdot50}$, the "half-life". $A_{0.95}$, or some value near it, appears preferable to the arbitrary $t\lambda$ in BEVERTON and HOLT's yield equation.

It is interesting to note that although HOLT considers my use of $A_{0\cdot95}$ as "absurd", BEVERTON and HOLT (1957, p. 288) derive a mathematically identical expression

$$t_i - t_0 = 1/K \log\left(\frac{1}{1 - x^{\frac{1}{3}}}\right)$$

in which x is any given proportion of W_∞ and t_i is the age at which the specified proportion is reached. Thus t_i is equivalent to A_p and my derivation, but not interpretation, of the term apparently was already anticipated when I presented the concept in 1956 to the meeting of the International Commission for the Northwest Atlantic Fisheries at Biarritz (TAYLOR, 1958b).

HOLT's letter indicates he appreciates the potentialities of growth-temperature relationships. He points out that they may set probable limits to natural mortality and define growth-rates for animals difficult to age. Of even greater importance, by quantitatively relating biomass to an environmental factor, I believe we may be able eventually to abandon some fundamental premises of the "theory of fishing" in favour of more profitable hypotheses and to direct more attention to the environment, the multitudinous factors of which form a dangerously large gap between fishing theory and reality.

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In my first letter I maintained that a change in K could not by itself affect age composition and life-span. I did not say that it would not affect the size composition; on the contrary, it would always affect size composition, unless there occurred a proportional change in the mortality coefficient. The discerning reader will see that in Figure 17·22 to which TAYLOR refers, there is indeed a substantial shift in the position of the peak of yield per recruit curves as a function of fishing mortality, for a given size at first capture. This figure thus demonstrates, as was intended, the specific effect of changes in K (and only in K) on yields. It has since been realized, as indicated in contributions to the Joint Scientific Meeting of FAO/ICES/ICNAF in Lisbon, in 1957, and by TANAKA (1958), that these yield curves are really functions of the ratios M/K and F/K, that is the parameters of mortality and catabolism never appear alone but always in these ratios.

I do not understand TAYLOR's reference to the "further confusion by assuming that L_∞ remains constant with a change in E". Thus, I agree that E (H in my first letter) and K seem often to vary together, but not of course proportionally — if they did then L_∞ would not vary, whereas both intra- and inter-species growth comparisons nearly always show that K is high when L_∞ is low, and vice versa. In some cases, especially where there is a wide variation of these parameters, there is no doubt that the relation is real. In other cases — and I have found that the danger is greatest when making intra-specific comparisons — the apparent relation is generated by the method of estimating these parameters from growth curves. Thus if l_t is plotted against l_{t+1}, as is the common practice, rotation of the regression line about the mean values, as a result of sampling or other variation, produces negatively correlated values of K and L_∞.

It should be noted that if there is an inverse relation between K and L_∞ it is such as to tend to nullify the effect on yield assessments of changes in K alone, whether these are caused by temperature or other factors. Thus if L_∞ and W_∞ had been varied in this way in the calculations from which Figure 17·22 was drawn, the three curves shown would have been much closer together. The positions of their peaks in terms of the fishing mortality coefficient would have been unaffected, but predictions of the effect on an observed yield of a given change in fishing intensity would have been little different from that which would have been predicted if both K and W_∞ had been assumed constant.

The variations of K and L_∞ or W_∞ with temperature are now beginning to be well documented, first for cod and now for razor clam by TAYLOR (1959), but also for other species and groups. Contributions to the World Scientific Meeting on the Biology of Sardines and Related Species (Rome, 1959) which summarize population data for species of *Sardina*, *Sardinops*, and *Sardinella*, give several instances of increasing K and decreasing L_∞ with decreasing distance from the Equator (summarized by HOLT, 1959). Perhaps more important at this stage is the possible relation between K and M. BEVERTON and HOLT (1959) have recently surveyed the published data and believe they have found evidence of the existence of a characteristic value of the ratio M/K for certain taxonomic groups of fishes. This seems to hold for a single species in different parts of its range, so that in warmer water a population has a lower L_∞ but higher K, and also higher M than in cooler water. This again is a relation tending to nullify the effect of temperature on the shapes of yield curves, which are determined principally by the value of M/K.

I am afraid TAYLOR has misunderstood my first letter when he says I concede that the knowledge of growth-temperature relations "may set probable limits to natural mortality". I referred specifically to growth/natural mortality relations, saying that if comparative studies revealed correlations between these two parameters, then we should have a means of using K to estimate probable values of M when the latter could not otherwise be determined. We cannot, however, circumvent such a study by calculating an equivalent age from a growth curve, calling the answer "life-span", and believing we have thereby estimated a mortality rate. The equation quoted by TAYLOR which gives the age at which a certain proportion of the asymptotic size is attained is merely a transformation of the growth equation to show that such a measure of what has been called the "physiological age" is simply, *by definition*, proportional to the reciprocal of K, which is an index of the rate of completion of the growth pattern. This has no reference whatever to mortality rates, and it is a pity that TAYLOR has repeated the same error in his otherwise admirable paper on razor clam growth.

The reason for my consideration of size at maturity is that this quantity can be directly measured rather easily in many fish, and if it has a consistent relation with the growth parameters it would be possible to predict the latter from maturity studies of fish the age of which cannot be determined. There is frequent mention in fisheries biological literature that maturity is reached at about two-thirds of the "final size". If "final size" is defined more precisely as L_∞, and the mean or median size of maturity as L_m, we find that an average value of L_m/L_∞ for many species is about 0·6 to 0·7, and if that were the whole story we should be able to estimate L_∞ without the need for age determination and construction of growth curves. Since several workers, especially GULLAND (1956), have shown that stock assessments can be made from knowledge of length compositions (in effect to estimate the ratios F/M and K/M) if L_∞ is known, this would suggest a means of carrying through a complete assessment in the absence of separate measures of growth and mortality parameters.

In practice the problem is more complicated because Lk/L_∞ is not constant but seems to vary with K; that is fish which complete their growth pattern more quickly (high K) mature at a size which is a greater proportion of their asymptotic size than those which unfold their growth pattern slowly (low K). The relation does not depend on the absolute magnitude of L_∞, so that "small" species which become adult in a year or so, and "large" species such as tunas, also with high K values, mature when they are more nearly full grown than, say, sturgeons, with low K values, which mature when they are less than half their full size. Certainly, in pursuing such studies we could tabulate $A_{0{\cdot}50}$, $A_{0{\cdot}95}$, or any other transformation instead of K, but to no particular advantage, because we should still be dealing with parameters of growth and not of mortality. There is, however, a *disadvantage* in adopting such a transformation for this particular purpose. Thus it might be overlooked that growth curves express a deterministic or an average relation, and in considering to what extent maturity is a function of age *or* of size or both, we need to examine the departures from the average — to see for example whether the mature fish of a certain age are smaller, or larger, than immature fish of the same age, and conversely whether mature fish of a certain size are older or younger than immature ones of the same size.

I believe the "fundamental premises" of the theory of fishing are that fish

breed, grow, and die, and that measurements of the rates of these processes or the relations between those rates, either direct or indirect through their common relation with such quantities as population density, food abundance, and measures of other environmental factors, can be used to compute the changes in characteristics of catch which would be expected to result from changes in fishing practices. I do not believe the time is ripe to abandon these premises. Our methods of estimating parameters, of making predictions, and particularly of testing and verifying or rejecting predictions, are, however, still inadequate to the demands now being made for advice on scientific conservation measures.

In a recent discussion of the "ecological diagnosis of a species" KESTEVEN and ROSA (see Proc. Gulf Caribb. Fish Inst., 11th Sess., p. 141, 1959) have again made a plea for the initiation of systematic comparative studies of marine populations, particularly of commercial species. TAYLOR has done just that, and it is because it seems to me that such studies can be of the greatest practical importance, and might even be the key to some of our present difficulties — as in earlier days comparative anatomy clarified problems of human anatomy — that I have taken up these issues with him, in the hope that other workers in this field will perceive more clearly what we both seem to be groping for.

Finally, may I draw attention away from TAYLOR's rather negative proposal to try to abandon the fundamental premises of the theory of fishing by focusing it on his more positive suggestion that more attention be paid to the environment. With this I agree, though do not think I agree that its manifold influences cause a dangerously large gap between fishing theory and reality; at least, it does not seem that evidence of a correlation between a population parameter and an environmental factor should be a cause of worry. Surely, at this stage in our work, we need to continue to develop methods of estimating population parameters, to compile the values obtained for comparative purposes, and to relate these quantitatively to the environmental parameters which are being compiled by oceanographers. But we need, simultaneously, to develop the theoretical basis for interpreting and using what would otherwise be an incoherent and indigestible mass of information. It is the use of a particular theory of fish growth which is enabling TAYLOR and others to begin sorting this information and take the first steps in constructing a model of an exploited fish stock in which the primary parameters are themselves functions of relevant factors of the physical and of the biotic environment. TAYLOR's success in this is encouraging us to continue, and indeed to intensify, our work in FAO, on the systematic compilation of population and environmental parameter values from published data, according to a plan being gradually and carefully worked out with collaborating biologists. We hope in this way to contribute to the formulation of practically useful quantitative generalizations, soundly based on the wide range of facts now being found and published at an accelerating rate by the world's rapidly increasing population of fisheries scientists.

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Reviews

Heezen, B. C., Tharpe, M., & M. Ewing. "The Floors of the Oceans. I. The North Atlantic". Geological Society of America, Special Paper 65, pp. 1–122, 49 Figs., 30 Pl. 1959.

A necessary stage in scientific progress is to fit together the available information into as coherent a picture as possible and to make the account easily available to other workers. It is fitting that a geological review of the North Atlantic (17°N to 50°N) should have been made by members of the team at the Lamont Geological Observatory, which has done so much to inform us of its structure, and that the paper should have been published by the Geological Society of America. The authors propose treating the other oceans in a like manner at a later date.

For the North Atlantic, they summarize evidence on the shape and composition of the floor, derived from soundings, samples, photographs, and by geophysical techniques and suggest its probable significance. The account is lavishly illustrated and there is a large physiographical diagram to give a first impression of the relief.

In view of the still small amount of information which is available it is not surprising that some of the authors' syntheses may not be completely acceptable. The brave suggestion that there are morphological steps on the sides of the Mid-Atlantic Ridge calls for further investigation. Likewise, many more intermediate sounding lines are required to define adequately the real extent of the deep valley, recognized at some places near the crest of the ridge. The presence of a number of valleys in many places and even of a blind ending valley, leads one to be chary of accepting too readily the continuity of any single valley. The authors recognize benches on the eastern continental slope of the United States, correlate these with major rock groups of different hardness and conclude that the features are erosional in origin. It will certainly be of great interest to establish this correlation firmly, both for American and other continental slopes. The signs of erosion on the continental slopes are now rather clearer but the relative importance of the agents suggested has still not been worked out, and it is not known whether they are still in operation. It may be that the effect was largely produced during the Pleistocene, for if it were of any importance before that time it is not clear how the observed thick pile of Cretaceous and Tertiary marine sediments could have accumulated at the edge of the continent.

The paper is a stimulating and attractive account of fact and interpretation which will probably be the basis of future geological work in the Atlantic and elsewhere for some time to come.

A. H. Stride

A. Remane & C. Schlieper. "Die Biologie des Brackwassers". Sammlung "Die Binnengewässer", Vol. 22, 348 pp. Price 55 DM. Stuttgart, 1958.

This book about the biology of the brackish water is written by the two well known professors from Kiel, ADOLF REMANE and CARL SCHLIEPER, who have carried out extensive studies on organisms from brackish water within their special field. In fact, the book consists of two completely independent parts, each written by its own author. The first part deals with the ecology of brackish water and is written by Professor REMANE; the second part deals with the physiology of brackish water, that means the physiological characteristics of organisms in brackish water, and this part is written by Professor SCHLIEPER.

The first part gives a survey of the concept of brackish water, its division and its hydrographic character. It is followed by a description of the ecological characteristics of organisms from brackish water, for example, the changes of size of these organisms, their morphological deviations, their reproduction, etc. In one chapter the occurrence of limnetic and marine organisms in brackish water is mentioned, together with the occurrence of the specific brackish water organisms. In another chapter the brackish water is divided into areas covered with plants, sand bottom, muddy bottom, and plankton, and the special character of these spheres of life is described.

The author finishes the first part by surveying different types of brackish water, including the Baltic Sea, the Black Sea, Caspian Sea, and the Aral Sea. Lagoons and brackish water in the mouths of rivers and in puddles are also described. This part of the book is illustrated with 81 figures and is easy to read.

Professor CARL SCHLIEPER introduces the second part, the physiological characteristics of life in brackish water, with a review of the varying content of salt and the osmotic resistance of the organisms. He tells about the activity of animals from brackish water, their rate of development, and their growth. He deals with osmoregulation and the ionic composition of the body fluids. The brackish water organisms' requirement of oxygen and their respiration is mentioned in detail in a special chapter. A survey of the permeability of the surface of the organisms, the temperature resistance, etc. is also given. The second part is illustrated with 58 figures and many tables, and it is clearly written.

"Die Biologie des Brackwassers" shows that the two authors personally have studied organisms from brackish water for a number of years and that they have the ability to treat their topics in an interesting way. Both parts are very thorough-going. They give a well balanced survey of the topics treated with a strong regard to both German and foreign literature. The aim has been a comprehensive information on the problems, not a rattling off of facts. The book can be recommended both to marine biologists and to limnologists.

Kaj Berg

Editorial Notice

"Current Bibliography for Aquatic Sciences and Fisheries".

As indicated in a previous note (*Journal du Conseil*, Vol. **24**, No. 3, pp. 497–98) the above periodical, prepared by FAO, is now being issued in printed form by the London publishers, Messrs. Taylor and Francis, Ltd. The mimeographed issues of Volume 2 have been, or will of course be sent free to all institutions which receive this Journal, as FAO kindly agreed in discussions during 1959. The printed form (starting from Vol. 3) will be available by subscription only, except to a few institutions collaborating substantially in the preparation of the Bibliography and to the Secretariats of other interested international organizations, including ICES.

It has been necessary to take this step because the costs of free distribution have increased greatly since its inception in 1958 as the combined result of the steady, year-by-year growth in the volume of literature pertaining to fisheries, limnology, oceanography, and marine biology, of the increase in coverage, and of the growing demand for the Bibliography by institutions and individual workers.

Thus FAO, while continuing to produce a manuscript, primarily for its internal use, has not the facilities or funds to distribute it widely. It will, however, be possible to continue improving the coverage and promptness of the FAO Current Bibliography, especially as we are informed that many periodicals are now received in Rome for annotation at proof stage. FAO will continue to devote as much staff and funds as possible to provide the basis for a satisfactory world-wide bibliographic service for marine scientists (and, of course, limnologists too). The International Council is collaborating in preparing current subject indices for the Bibliography following, for the time being, the classification used in the arrangement of the Council's Current Bibliography in this Journal, now discontinued. This arrangement will be reviewed by FAO and ICES from time to time, and meanwhile FAO is taking steps to increase the number of subscribers to the Bibliography and in other ways make it possible for the subscription rate to be reduced. It should be pointed out, nevertheless, that because the considerable cost of compiling the manuscript of the Bibliography is borne by FAO its printed form can be offered for sale at a very much lower price than is normally possible for abstracting and bibliographic publications in other fields of science.